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Stratégies d'exploration racinaire et cycles des nutriments :

Étude du rôle fonctionnel de l'exploration horizontale du sol par les plantes

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Première partie .

Introduction et synthèse bibliographique

Introduction

Cette thèse se situe dans le cadre de l'étude des **stratégies de nutrition des plantes**, plus particulièrement dans les écosystèmes dont la productivité primaire est limitée par la disponibilité des nutriments minéraux du sol comme l'azote ou le phosphore. Au sein de ce cadre, mon objectif général est de chercher à comprendre les interactions entre deux processus par lesquels les plantes acquièrent des nutriments : d'un côté le **développement de l'appareil racinaire** comme moyen de prospection du sol et de l'autre le **contrôle de la disponibilité des nutriments** en influençant la vitesse du recyclage des nutriments, les entrées et les sorties de nutriments, l'accessibilité des nutriments déjà présents**.** Cela passe par la mise en place de rétroactions complexes entre les racines, le sol (matière organique et propriétés physico-chimiques) et les organismes du sol. Pour répondre à cet objectif, j'adopte une **approche spatialisée**, autour de deux concepts :

- L'**exploration du sol**, qui exprime le fait qu'au travers du développement de leur système racinaire, les plantes développent une surface d'échange et d'interaction avec le sol, dans un volume fini.
- L'**occupation du sol**, définie comme la capacité des plantes à contrôler le fonctionnement du sol dans le volume qu'elles explorent et en particulier l'augmentation locale de la quantité de nutriments disponibles.

Dans le chapitre de synthèse bibliographique qui suit cette introduction, je définis ces deux concepts plus en détail – ainsi que tous les autres termes mis en gras dans ce paragraphe – et explicite les processus par lesquels les plantes sont capables d'influencer les cycles des nutriments ainsi que leurs échelles spatiales et temporelle respectives. Je considère ensuite la relation entre occupation et exploration à deux échelles distinctes. Celle de l'action à court terme de racines dans une portion de sol exploré par une plante (la **rhizosphère**) et celle de l'interaction à plus long terme des plantes avec le sol, par l'ensemble de leur système racinaire (la **zone d'influence souterraine**). A l'échelle de la rhizosphère, je propose l'hypothèse qu'il peut exister une **synergie entre les racines d'une même plante**, dans la mobilisation et l'absorption des nutriments. A l'échelle de la zone d'influence, je propose l'existence d'un compromis entre la taille du volume de sol exploré par une plante et de sa capacité à y contrôler le cycle et la disponibilité des nutriments limitant, plus simplement appelé **compromis entre exploration et occupation du sol**. Ce chapitre de synthèse bibliographique est rédigé sous la forme d'un article en anglais, afin que le

cadre général de cette thèse soit plus accessible aux lecteurs non francophones et en vue d'une valorisation sous forme d'article.

Au cours de cette thèse, **3 axes méthodologiques distincts ont été développés**, chacun faisant l'objet d'un chapitre distinct : la **modélisation mathématique** (**chapitre 2**), l'**étude des interactions plante-sol** *in situ*, sur le terrain (**chapitre 3**) et la **modélisation numérique** (**chapitre 4**). Chacun des chapitre est rédigé sous forme d'un article en anglais, précédé d'une introduction en français. Les pistes de travail émergeant de chacune des approches sont l'objet d'une partie de perspectives à la fin des chapitres. Dans le chapitre 2 je cherche à déterminer sous quelles conditions des plantes tireraient un avantage en restreignant l'exploration du sol. Le chapitre 3 est une étude des relation entre patron d'exploration racinaire et contrôle des cycles des nutriments, chez 3 espèces de Poacées pérennes de savane. Le chapitre 4 teste l'hypothèse de la possibilité de synergie entres racines pour une plante capable influençant la disponibilité du phosphore par l'exsudation de citrate.

Une discussion et une conclusion générales font enfin le bilan de l'apport de chacun des axes à la problématique générale de thèse. J'y propose également de nouveaux axes de recherches permettant d'approfondir et de valoriser la question de l'interaction entre le contrôle du recyclage des nutriments et les stratégies d'exploration racinaire.

1. Integrating plant control of nutrient cycling within root foraging strategies

1.1. Introduction

The productivity of terrestrial ecosystems relies on the access of plant communities to limiting resources such as light, water and nutrients. Soil plays a key role in plant nutrition and has been the object of most of the emblematic inventions of agriculture, from the plough to chemical fertilizers. Despite undeniable increase in productivity, modern intensive practices that started during the last industrial revolution strongly impact the cycling of nutrients (especially nitrogen and phosphorus) within terrestrial ecosystems (Vitousek et al., 1997; Bennett and Elser, 2011), leading to a plea for more sustainable practices (Tilman, 1999). Ecology and soil sciences are particularly mobilized in this context. In the study of "agro-ecosystems", they contribute to the development and assessment of new, low-input practices (Weiner, 2004). Upstream, the study of plant-soil system functioning within "natural" ecosystems, and especially, the strategies of wild plants to acquire mineral nutrients (Craine, 2009), is also a potential source of inspiration (Malézieux, 2011). The work presented in this thesis falls within this last approach, **with a focus on ecosystems where the productivity is limited by soil nutrients such as nitrogen and phosphorus**.

The development and activity of the root system have a major role in the nutrient acquisition strategies of plants. The concept of **root foraging strategy** describes the adjustment of root systems to the characteristics of the soil in which they grow in ways that optimize the uptake of available nutrients (McNickle et al., 2009; de Kroon and Mommer, 2006; Mordelet et al., 1996). In the past decades, most studies on the subject focused on adjustments to the heterogeneity of soil resources and the presence of competitors (Hodge, 2004, 2006; Mommer et al., 2011). However, nutrient acquisition strategies of plants do not only consist in getting available nutrients where they are (Craine, 2009). Among other mechanisms, studies on **plant-soil feedbacks** (Ehrenfeld et al., 2005; van der Putten et al., 2013; Hobbie, 1992) have underlined the ability of plants to actively influence soil functioning and alter nutrient availability. Some authors even developed the concept of **active control of nutrient cycling** within the soil (Chapman et al., 2006). The ability of plants to alter nutrient cycling in soils relies on a wide range of

mechanisms, including root exudation (Dakora and Phillips, 2002). Still, root foraging studies often consider roots as organs specialized in the uptake of nutrients and neglect their ability to produce exudates (*e.g.*(Cahill and McNickle, 2011; McNickle et al., 2009)). A general goal of this thesis is to **explore the links between plant control of nutrient cycling and root foraging strategies** to address general questions such as: **to what extent the ability of plants to influence nutrient cycling is involved in root foraging strategies? What are the consequences of soil exploration patterns of roots on nutrient cycling within the plant-soil systems?**

The **spatial and temporal patterns of plant-soil interactions** are important pieces of information in the understanding of nutrient acquisition strategies of plants (Jackson and Caldwell, 1993; Ettema and Wardle, 2002). As plant are sessile organisms, their access to pools of nutrients is directly constrained by the extension of the root system within the soil. In this thesis, I will use **"soil exploration"** to describe the finite volume of soil circumscribed by plants during the development of their root system (Huston and DeAngelis, 1994). However, the full access to the pool of nutrients contained within this volume depends on plant ability to control nutrient cycling, as all the present nutrients are not directly available. I will therefore use the term **"soil occupation"** to describe the ability of plant to control nutrient availability within a given volume of soil explored. In this thesis, I use the distinction between soil exploration and occupation as a heuristic way to articulate plant control of nutrient cycling and root spatial patterns.

Before the presentation of the work packages of my thesis, the aim of this review chapter is threefold:

1. To list the processes by which plants influence nutrient cycling within the soil (figure 1.1).
2. To quantify their respective temporal and spatial scales, in order to have a better understanding of their interplay with nutrient uptake.
3. To formulate hypotheses on the consequences of the root exploration patterns on nutrient cycling within the plant-soil systems and on how the control of nutrient cycling could be integrated within nutrient foraging strategies.

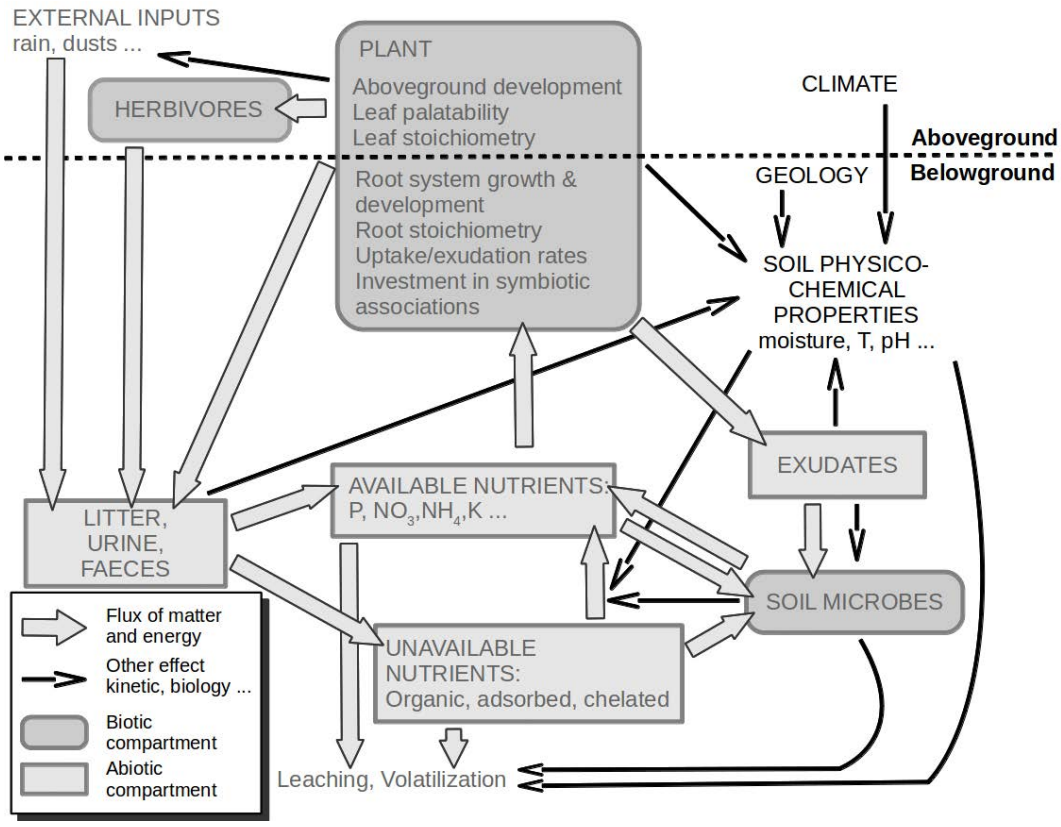

Figure 1.1.: Schematic representation of the interplays between plant nutrient strategies, plant-soil interactions and nutrient cycling.

1.2. Plants ability to control nutrient cycling

I define **plant control of nutrient cycling** as the ability of a plant (1) in flux and outflow of nutrients, (2) the availability of nutrients already present in the soil through changes in the state of nutrients (solubilization, mineralization, nitrification ...)(Lambers et al., 2008; Lata et al., 2004; Hinsinger, 2001). Available nutrients consist mainly in mineral nutrients dissolved in the soil solution, although in some nitrogen-poor systems, plants are also able to take up directly dissolved organic nitrogen such as amino-acids (Jones et al., 2005). A large share of nutrients contained within the soil are not available for direct uptake by roots, being either in a wrong chemical form (*e.g.* complex organic molecules), chelated or adsorbed to the soil solid phase (Binkley and Vitousek, 1989; Hinsinger, 2001). These nutrients can be rendered available by biogeochemical reactions such as mineralization or solubilization. The thermodynamic equilibria and kinetics of these reactions are a function of soil physico-chemical properties and biological activities (figure 1.1). This section reviews the mechanisms by which plants affect nutrient cycling, either through a direct effect on nutrient fluxes or soil chemical properties, or indirectly with the mediation of soil micro-organisms. I also consider the specific case of plant interactions with large herbivores that are also involved in this thesis.

1.2.1. "Direct" control of nutrient availability

Aboveground, plants contribute to the formation of humus through the deposition of their own litter or the interception of organic particles brought by wind or rain flow (Ehrenfeld et al., 2005). In addition to this influx of organic matter, micro-climatic conditions due to the combined effects of canopy and litter affect soil physico-chemistry (Ehrenfeld et al., 2005).

In the same way as aboveground litter, root mortality brings back to soil organic matter that releases mineral nutrient through its decomposition (Silver and Miya, 2001). In some nutrient-poor ecosystems, the recycling of nutrients contained in roots can represent a significant share of plant productivity (Abbadie et al., 1992). Rhizodeposition is a more active process by which plants influence nutrient cycling belowground (Haichar et al., 2014). It includes root exudates (light organic molecules that diffuse passively from the roots), mucilage, border cells and gases (Haichar et al., 2014). For example, root exudation modifies the precipitation-dissolution equilibria of phosphorus through the modification of soil pH (Hinsinger, 2001).

Plant take nutrients from the soil solution, the nutrient concentration of which differs from total nutrient concentration within the soil (including all soil phases)(Craine, 2009). As a consequence plants indirectly affect nutrient availability through their influence on soil water content: the more water there is in the soil, the more diluted (and thus the harder to take up) nutrients are.

1.2.2. Interaction with soil microbes

As meant by the expression "microbial bottleneck" (Chapman et al., 2006), plants are often dependent on soil microorganisms such as bacteria, fungi or archea that mineralize soil organic matter (SOM). By extension, they also depend on soil fauna that is also involved in SOM mineralisation (Bardgett and Chan, 1999), but this aspect will not be developed further in this thesis. The exudation of carbohydrates is a way by which they can boost this process and access to nutrients within recalcitrant pools of SOM ("rhizospheric priming effect"(Fontaine et al., 2007)). However, a plant benefits from the microbial loop (Coleman, 1994) directly only if the microorganisms involved are not themselves limited by nutrients. This is constrained by litter (or exudates) stoichiometry (especially the C:N ratio): microbes release mineral nutrients into the soil solution only if the ratio of carbon to nutrient of litter (or exudates) is sufficiently low (Ehrenfeld et al., 2005). Otherwise, nutrients are immobilized within the soil microbial biomass after mineralization. Soil microorganisms are also competitors for nutrients. Hence, mechanisms involved within scramble (*e.g.* nutrient preemption) or interference (allelopathy) competition

between plants or between plants and microorganisms are also ways by which a plant can control nutrient cycling efficiently (Lankau et al., 2011). This issue is not developed directly in the main part of this thesis but will be tackled in the general discussion (section 5.2.3).

Due to their specific biochemical pathways, chemo-heterotrophic microorganisms – requiring preformed organic compounds as a source of carbon and oxidizing organic compounds as a source of energy – may affect nutrient availability in other ways, often because what is a nutrient for the plant is actually waste for the microorganisms. In the case of the nitrogen cycle, denitrifying microorganisms contribute to losses of nitrogen for the plant-soil system by the volatilization of N_2O (Marschner and Rengel, 2007; Roberston, 1989). Nitrifying bacteria transform ammonium into nitrate (Kowalchuk and Stephen, 2001). This has two main consequences: (i) it affects plant nutrient uptake depending on their preference for ammonium or nitrate (Boudsocq et al., 2009, 2012) and (ii) nitrate is more mobile than ammonium in most soils, and thus more submitted to leaching, or can be lost through denitrification (Kowalchuk and Stephen, 2001). Plants are sometimes able to control such bacterial activities, as exemplified by the biological nitrification inhibition (BNI)(Lata et al., 2004; Subbarao et al., 2006). This control is made by the exudation of secondary metabolites that inhibit the growth and activity of nitrifying bacteria (Subbarao et al., 2006).

A last way for plants to control nutrient cycling is the formation of symbioses with microorganisms, especially nitrogen-fixing bacteria and mycorrhizal fungi (Bonfante and Anca, 2009). Nitrogen-fixing bacteria create an additional input of nitrogen to the plant-soil system. As hyphae substitute for roots in soil exploration, mycorhizal fungi give a direct access to pools of otherwise unavailable nutrients, in particular by a considerable increase of their surface of interaction with soil (Hodge and Fitter, 2010; Veresoglou et al., 2012; Chapman et al., 2006). Mycorhizal fungi are also known to affect different reactions of the nitrogen cycle (Veresoglou et al., 2012). The role of mycorrhizae within nutrient foraging strategies is well developed in the literature (Hodge, 2006; Croft et al., 2011; Tibbett, 2000) but the interaction of hyphae with soil can be quite different from that of roots alone. In this thesis I focus on root foraging strategies and discuss the generalization of my results to the case of mycorrhizae in the general discussion (see section 5.2.1).

1.2.3. Interaction with large herbivores

Large herbivores have two main effects on plant nutrition: on the one hand, the consumption of plant material creates an additional demand for nutrients, while on the other hand, dung and

urine are an important source of rapidly available nitrogen for plants, and affect the kinetics of nitrogen cycling reactions (Ambus et al., 2007; Coetsee et al., 2010). They also affect soil functioning by trampling (Augustine et al., 2003). Overall, their effect on nitrogen cycling is complex, and depends on herbivore density (McNaughton, 1979; de Mazancourt et al., 1998), body mass, and digestive type (*e.g.* ruminants *vs.* non ruminants). Still, plants can regulate their consumption by herbivores, for example through leaf palatability (C:N ratio, tannins production)(de Mazancourt and Loreau, 2000; Robbins et al., 1987) or through the production of structural defences against herbivores (Cooper and Owen-Smith, 1986).

The regulation of leaf palatability can be considered as part of a strategy to control nutrient cycling (de Mazancourt and Loreau, 2000; Craine, 2009), but one has to take into account the distinction between the areas where herbivores consume plants and those where they evacuate dejections (de Mazancourt and Loreau, 2000). When these two locations match, the association of plant and herbivores can lead to areas, characterized by a specific flora and high nitrogen cycling rates, called grazing lawns (McNaughton, 1986). Other plants have a very low palatability but may benefit from dung and urine deposition, by providing a temporal shelter for herbivores at the scale of individual trees or a hiding place at the scale of a community of tall tussock grasses.

1.3. The spatial and temporal scales of plant-soil interactions

I will develop here three scales of plant-soil interactions, depending on whether one considers the effect of individual roots, the functioning of the overall root system, or takes into account aboveground effects of plants on soil. For each scale, I will give a definition and the associated spatial and temporal orders of magnitude (o.m.). All this information is summarized in table 1.1.

1.3.1. The rhizosphere

The **rhizosphere** is defined as the volume of soil directly influenced by living roots (Hiltner, 1904; Hinsinger et al., 2005, 2009; Cardon and Whitbeck, 2011), as opposed to bulk soil. **This concept has to be used with caution**, due to the two following characteristics (Hinsinger et al., 2009):

- **There is no real border to the rhizosphere**. The influence of roots on soil consists in building concentration gradients so there are continuous changes in water and solute

Table 1.1.: Summary of the various scales of plants-soil interaction and their respective order of magnitude (o.m.)

Scale	Processes involved	Spatial o.m.	Temporal o.m.
rhizosphere	nutrient uptake, exudation	mm - cm	second - day
belowground zone of influence (ZOI)	root development, root mortality	cm - 10 m	month - 10 year
aboveground ZOI	litter deposition, micro-climatic effect, interception/accumulation by the canopy	m - 10m	month - 10 year
extended aboveground ZOI	deposition of dung and urine by herbivores	m - 10 m	week - 10 year

concentrations from the root surface to the bulk soil.

– For a given portion of root, **there can be as many different rhizospheres as there are processes and solute considered**. The distance over which a root influences soil is not necessarily the same if one considers nutrient depletion or accumulation near the root surface, exudation, gradients of soil microbial composition or activity etc. For processes involving the diffusion of solutes, the size of the rhizosphere increases with their diffusive ability (Ge et al., 2000) and so with soil water content.

Even if some experimental settings allow its visualization *in situ*, the rhizosphere is not easy to measure in the field (Hinsinger et al., 2009). Modelling is a useful tool to estimate volumes of soil influenced by roots, taking into account the diffusion of solutes within the soil solution (Tinker and Nye, 2000; Ge et al., 2000; Raynaud, 2010). These approaches show that the rhizosphere is a very small volume; individual roots generally influence the soil to a distance of a few millimetres (Hinsinger et al., 2005). Depending on the process considered, only specific sections of the root system interact with soil (Doussan et al., 2003; Hinsinger et al., 2005). For example, nitrate active uptake occurs mainly in the apical zones (Lazof et al., 1992).

From a temporal point of view, the rhizosphere can be considered as a volume that evolves relatively quickly with soil water content – which affects diffusion rates of soil solutes within the soil (Tinker and Nye, 2000) – and with the development of the root system. One also has to consider the potential delay (depending on the microclimatic parameters of plant/soil eg. water or T°) between the effect of root exudation on soil functioning (*e.g.* priming effect (Epron et al., 2011)) and its benefits for the plant (increased concentration of available nutrients). This delay should also depend on the type of control (direct or involving rhizosphere bacteria). Potentially,

a portion of root might take up nutrients that were made available by another portion. This underlines the necessity of integrating root-soil interactions at the scale of the whole root system.

1.3.2. The below-ground zone of influence

The **zone of influence (ZOI)** has been defined as the area over which a plant alters its environment, either above- or below-ground (Casper et al., 2003). The difference with the rhizosphere is that here other mechanisms than the direct effect of living roots are involved. At the scale of the belowground ZOI, plant influence on soil functioning emerges from the combination of the different effects of individual roots and their respective rhizospheres and the development of the root system.

A first approximation of the dimension of the belowground ZOI is given by measuring the **distribution of root biomass** at a given time. This can be done either directly by excavating whole roots systems (*e.g.* (Guevara et al., 2009)) or by sampling the soil with a regularly distributed pattern (Lata et al., 2000), or indirectly by using tracers (Casper et al., 2003; Hartle et al., 2006). Maximum lateral spread, and rooting depth give an idea of the whole volume explored by plants (Schenk and Jackson, 2002; Casper et al., 2003).

In a given volume of soil, the surface of interaction between plant and soil is a function of **root density** (mass of roots per mass or volume of soil) but is more accurately described by **root length density** (cumulated length of roots per mass or volume of soil). Roots can vary in their **specific root length** (SLR – root length developed per unit of root biomass). At a finer scale the exchange surface of roots can be enhanced by structures such as root hairs (Gregory, 2006). "Cluster roots" that are especially found in the Proteaceae family, is an extreme case of such surface development (Lambers et al., 2006). **Root architecture** – the topological organisation of root length within the soil volume – gives additional information to the understanding of plant-soil interaction in the belowground ZOI (Hodge et al., 2009; Pagès, 2011). In particular, it determines potential overlapping between the rhizospheres of different portions of roots (Pagès, 2011).

Root demography – the dynamic of growth and senescence of roots – within the belowground zone of influence also has to be considered. The belowground ZOI is a volume in which a plant can easily grow new roots or where its dead roots can be found. The temporal dynamics of the root system can be evaluated *in situ* by the use of rhizotrons (Gregory, 2006). The lifespan of roots is highly variable, some roots remaining through the whole plant life and other structures such as cluster roots being short-lived (Eissenstat and Yanai, 1997). Considering root

mortality, a growing root can benefit from the influence of a dead root within the soil explored (see subsection 1.2.1). The organisation of soil aggregates favours the growth of a young root in the reliquary rhizosphere of a dead root.

1.3.3. The above-ground zone of influence

The aboveground ZOI is *a priori* simpler than the belowground ZOI. Aboveground, plants affect the most superficial layers of soil, through the deposition of aerial litter, the interception of litter, dust or rainwater and a micro-climatic effect. The aboveground ZOI is generally smaller than the belowground ZOI (Casper et al., 2003). Aboveground architecture is much more constrained physically than belowground architecture: contrary to branches, roots can grow at several decameters from plant stem Mordelet et al. (1996); Schenk and Jackson (2002). The aboveground zone of influence should be relatively stable with time, apart from phenological changes largely determined by seasonality (summer *vs.* winter or wet *vs.* dry season) or perturbation such as fire or herbivory (Abbadie et al., 2006).

1.3.4. Extended above-ground zone of influence

One can also consider an extended definition of the aboveground ZOI that includes plant interaction with herbivores. If a plant favours the presence of a herbivore, *e.g.* through palatability or shading, it may indirectly favour a positive feedback on soil functioning over an area larger than that directly influenced by its canopy, but under which its roots can grow. Grazing lawns are an example where plants, in interaction with herbivores, create a zone functionally distinct from surrounding tall grass areas (McNaughton, 1984).

1.4. Linking plant control of nutrient cycling to root foraging strategies

From the previous section, soil exploration can be characterized by the size and shape of the belowground ZOI, while soil occupation is the outcome of the dynamics of the rhizosphere within the ZOI and the interaction between the above- and belowground ZOIs. Here I will show how soil exploration and soil occupation can be articulated within root foraging strategies. **In a first subsection**, I will **list plant traits that may affect the intensity of soil occupation and exploration** and are likely to be selected within

a nutrient acquisition strategy. **Second**, I will consider the **multiple effect of roots on soil** and their implications in **the relationships between root density and nutrient cycling within the soil**. Last, I will consider the **integration of plant-soil interactions at the scale of the below-ground ZOI**.

1.4.1. Root traits involved in root foraging strategies

A first, relatively obvious trait that affects both soil exploration and occupation is the allocation of carbon, nutrients and energy to roots, from which depends the overall root system size (biomass) and activity. A given quantity of root biomass can be spread over a wide range of horizontal or vertical distance (Jackson et al., 1996; Hartle et al., 2006; Schenk and Jackson, 2002; Casper et al., 2003). Root lateral spread and maximum rooting depth give the ultimate border of the soil explored by plants (Schenk and Jackson, 2002; Casper et al., 2003). I focused in my work on the horizontal distribution of roots. The relative size of the below- and above-ground zones of influence are also parameter that plant can adjust depending on the context. (Casper et al., 2003) showed that plants growing in arid soils tend to have a larger belowground ZOI compared to aboveground. The difference of size of the ZOI is also a parameter involved in the creation of islands of fertility – accumulation of carbon and nutrients below the plant canopy (Scholes and Archer, 1997).

The distribution of roots within the explored volume of soil is often heterogeneous. Part of this heterogeneity comes from an architectural development constraints that causes roots to concentrate near the plant stem (Casper et al., 2003). However, plants are also able to locally adjust root density and activities to the heterogeneity of nutrients (Hodge, 2004) and the presence of competitors (Gersani et al., 2001). Plant morphological and physiological plasticity potentially affect the degree of soil occupation. Some soil activities can be directly correlated to root density (*e.g.* (Lata et al., 2000)) and the geometry of the rhizosphere depends directly on the rates of uptake or exudation (see subsection 1.3.1).

Root system architecture is also subject to a wide range of variations among plant species, with implications for the efficiency of the root system functioning (Lynch, 1995). The same is true for the organisation of clonal species, which vary in the organisation of their ramets (Harper, 1977; Oborny et al., 2012). For example rhizomatous and caespitose grass species do not have the same impact on thesoil where they grow (Derner and Briske, 2001).

Life history traits are also important in plant-soil interactions. As an example, annual plants interact with a given portion of soil at shorter temporal scales and generally explore a smaller

volume of soil than biennials or perennials (Schenk and Jackson, 2002). At a smaller scale, root demography affects the duration of plant-soil interaction.

1.4.2. Relationships between local root density and soil functioning

Here I consider the interaction of a portion of the root system within a fixed soil volume. In this context, an *efficient* root foraging strategy can be defined as the co-occurrence of a root length density, an uptake rate and a level of exudation which together optimize total nutrient uptake rate. An *optimal* strategy maximises the benefits in terms of nutrient uptake with the lowest possible costs in terms of root construction and activity (Lynch and Ho, 2005). Root foraging strategy in the presence of competitors follows a different formalism (O'Brien et al., 2007), which is discussed at the end of this thesis (section 5.2.3).

Increasing root densities can lead to more overlap between the rhizospheres (Pagès, 2011; Ge et al., 2000), which may reduces the mean uptake efficiency. This possibility is described by applying the concept of competition to the roots of a same individual plant (Ge et al., 2000). Considering nutrient uptake only, the most efficient root systems should be the ones that minimize root overlap. However, the same portion of root affects the surrounding soil through different processes, including some that can increase nutrient availability. As the sizes of the rhizospheres depend on the process considered (subsection 1.3.1), there may be situations where exudation rhizospheres overlap, but not the depletion rhizospheres. In such a case, a plant may benefit from root proximity: a root may benefit from the positive feedback generated by a neighbour root. A hypothesis considered in my thesis is that **in cases where roots also increase the availability of nutrients, the overlap of rhizospheres may lead to synergy between roots.**

1.4.3. Root foraging strategies at the whole plant scale: hypothesis of a trade-off between soil exploration and occupation

The "Guerilla *vs.* Phalanx" metaphor was formulated in a context of competition for resources by plants to account for contrasted behaviours of clonal plants (Harper, 1980; Clegg, 1978) (figure 1.2A). A guerilla strategy maximises the discovery of new pools of resources, while the phalanx strategy is a better way to locally outcompete other plants. **In this thesis I will propose the use of the "exploration *vs.* occupation" distinction as a way to generalize the "guerilla *vs.* phalanx" metaphor to other plant-soil interactions than nutrient**

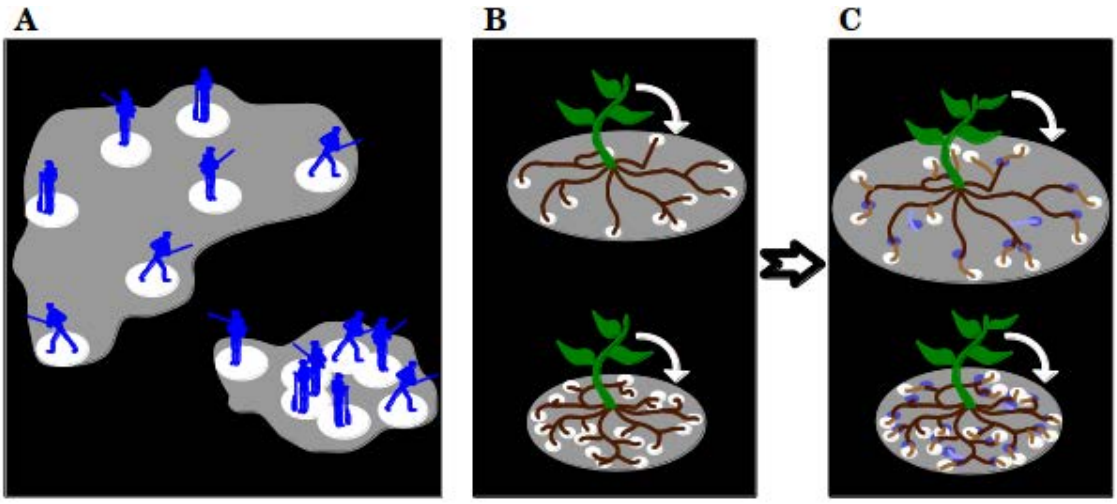

Figure 1.2.: Illustration of the distinction between exploration and occupation for plants, from the guerilla *vs.* phalanx metaphor (Harper, 1980; Clegg, 1978). Panel A represents a schematic battlefield, where the men of an army are either scattered over a large area ("guerilla" – top left) or crowded ("phalanx" – bottom right). Panel B &C transposes these distinction in the case of two plants following either a "guerilla" (top) or a "phalanx" (bottom) strategy at two successive times, mapping soldiers to individual roots. In both panels, the explored area is in grey and the zone controlled by individual soldiers/roots at a given time is in white. The white/grey ratio gives a quantification of soil occupation. In panel C, dead roots and previous rhizosphere are in blue. The white arrow figures the aboveground feedback of the plant on the soil.

preemption in a competitive context alone. Figure 1.2 shows how this metaphor can be applied to the exploration of soil by plants. In panel A, the explored area of the army (in light grey) expands when soldiers penetrate in the unexplored area (in black). At a given time, the area actually controlled by individual soldiers is in white. The guerilla strategy (top left) allows the exploration of a wide area with a low control of what happens inside, while the phalanx strategy (bottom right) leads to a smaller but better controlled explored area. Brown and violet lines respectively represent newly grown and dead roots, and the small blue ellipses represent the long-term feedback of previous rhizospheres on soil functioning. If this feedback is positive and dead roots are sources of nutrients, the degree of soil occupation by plants depends not only on the white/grey ratio but also on the proximity between the white and blue areas. Thus, as in the first panel, the "guerilla *vs.* phalanx" metaphor leads to the idea of a trade-off between exploration and occupation.

On the three panels of figure 1.2, the grey area quantifies the intensity of soil exploration while the white over grey area ratio is an approximation of soil occupation efficiency. From this schematic representation, different hypotheses can be made on the relationships between soil occupation and soil exploration. First, soil occupation decreases mechanically when soil

exploration increases, as root can only directly interact with a limited volume. Second, this effect should increase with the explored area as more and more root length is dedicated to structure and transport, and less to interaction with soil. Third, if the phalanx strategy is associated to slower growth of roots, the temporal dynamics of root development during exploration may further favour this strategy. The distance between old (blue) and new (white) rhizosphere is reduced. This means that if there is a delay between exudation from a portion of root and a resulting beneficial effect in terms of nutrient availability, plant would benefit more from this effect. Last, as already hypothesized by Abbadie and Lata (2006), the proximity between living and dead roots (in blue) may favour the uptake of nutrients diffusing from dead roots. All this can be summarized under the general hypothesis of a **trade-off between the extent of soil exploration and the efficiency of soil occupation**. In the followings, I will use the shorter **exploration/occupation trade-off**.

The exploration/occupation trade-off should lead to distinct root foraging behaviour in nutrient-poor conditions. Plant that specialise in the efficient uptake of readily available nutrients should adopt a guerilla-like strategy, especially if they are able to efficiently exploit nutrient rich patches of soil that are often short-lived. By analogy with the fact that below-ground zones of influence tend to be larger in water-limiting conditions (Casper et al., 2003), those plant should explore a wider area of soil to increase their pool of available nutrients. Plant that are able to increase the availability of nutrients and control nutrient cycling should on the contrary follow a guerilla-like behaviour, by investing more root biomass and exudates in a localized area.

1.5. Conclusions

This first, introductory chapter gave an overview of possible ways to link root foraging strategies to the control of nutrient cycling by plants. The review of the processes by which plants can influence nutrient cycling and in particular increase nutrient availability showed a wide range of mechanisms, most of which involving other living organisms, especially soil microbes and large herbivores. The second section on the scales of these processes showed that: (1) **the direct interaction of living roots with soil involved a variety of mechanisms with different rhizosphere sizes**; (2) **plant influence on nutrient cycling at the whole plant scale involves the articulation of various mechanisms with different spatial and temporal scales**. In the third section, I thus hypothesized that the **combined effect of root exudation and uptake may lead to synergy between roots** at high root densities. I also proposed

the existence of an **exploration/occupation trade-off**. I proposed that, as a consequence, the limitation of soil exploration can be an efficient strategy in nutrient poor ecosystems.

I structure my thesis in three distinct methodological axes, corresponding to the next chapters of this memoir.

1. The occupation/exploration trade-off hypothesis suggests that in some cases, plant could maximise the control of nutrient cycling by exploring a limited volume of soil (See 1.4.3). It would thus provide an original explanation to the contrasted root exploration pattern that can be observed in some ecosystems. *In the second chapter, I will develop a general model of nutrient cycling and soil exploration by a plant population, with the aim of determining under which conditions a restricted soil exploration patterns could be observed.*
2. Perennial grasses constitute an interesting biological model since they interact with the soil in the long-term through different patterns of soil exploration (rhizomatous *vs.* caespitose). Under the hypothesis of a trade-off between exploration and occupation, I expect caespitose species to control nutrient cycling in a better way than rhizomatous ones. *The third chapter aims at characterizing root exploration patterns and soil occupation empirically, for three species of grasses from a dry savanna (Hwange, Zimbabwe). This field work also allowed to assess the influence of nutrient limitation and herbivores on plant-foraging behaviour.*
3. The last chapter explores the hypothesis that the combination of root exudation and facilitation leads to synergy between roots. It also tackles the issue of scaling up nutrient cycling processes from the rhizosphere to the whole ZOI. *I develop a numerical modelling approach that quantifies plant-soil interaction at the two scales here-above described: the rhizosphere and the whole volume of soil explored by a plant. My aim is to determine relationships between root length densities and the control of nutrient cycling, and to assess which exploration behaviour these relationships should favour.*

Part II.

Pourquoi et quand les plantes devraient-elles limiter l'exploration du sol par leurs racines ?

Introduction de la partie

Le chapitre de synthèse bibliographique m'a permis de formuler l'hypothèse d'un compromis entre exploration et occupation du sol et a proposé qu'il soit le résultat de l'intégration à long terme des rétroactions plante-sol à l'échelle de la zone d'influence souterraine. A partir de cette hypothèse générale, j'ai formulé **l'idée qu'une limitation de l'exploration du sol puisse être une stratégie de nutrition efficace dans des écosystèmes pauvres en nutriments**. Dans ce chapitre, je me place dans cette perspective d'**intégration des interactions plante-sol à l'échelle de la zone d'influence souterraine**. Je construit à cette fin **deux modèles généraux du recyclage d'un élément limitant à l'échelle d'une population de plante**. Dans ce modèle, le compromis occupation/exploration est admis comme postulat, et la question est de savoir à quelles conditions il a un effet significatif sur les stratégies d'exploration racinaires. En particulier : à quelles conditions serait-il intéressant pour une plante de limiter l'étendue de son domaine d'exploration racinaire ?

2. Why and when should plant limit the exploration of soil by their roots?

(Submitted to *Oikos*)

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2.1. Abstract

1. In ecosystems limited by soil nutrients, some plants show a restricted horizontal distribution of their roots. We explore the hypothesis that this particular pattern is a foraging strategy emerging from trade-offs between soil exploration (that increases the pool of nutrients available for plants) and the local control of nutrient cycling within the soil.
2. We developed two general analytical models of the cycling of a limiting nutrient in a plant population. They explore how plant productivity is affected when roots do not exploit the whole soil available and try to determine the conditions for which plant biomass is maximized by a limitation of soil exploration.
3. We predict that a restricted exploration strategy is beneficial when (1) there is at least one trade-off between a nutrient cycling parameter and soil exploration, (2) unexplored soil is poor in mineral nutrients and (3) the volume of soil explored by plants is stable over time. The exploration limitation strategy results in spatially heterogeneous and nutrient-conservative ecosystems.
4. Our results should apply to numerous ecosystem types and, in particular for perennial grasses within tropical, nutrient-limited ones. Our study underlines the importance of considering the multiplicity of the effects of roots on soil and subsequent feedbacks in defining root foraging strategies.

2.2. Introduction

Root distribution within the soil affects the functioning of the plant-soil system at different scales. At the millimetre to centimetre scale, root density impacts nutrient-uptake efficiency,

but also plant feedbacks on nutrient availability and microbial activities through root exudation (Hinsinger et al., 2009). At the scale of individual plants, the pool of soil resources potentially available depends not only on the distribution of resources and their diffusion rates, but also on the size and the shape of the root system (Lynch, 1995; Pagès, 2011). At population and community scales, it determines the intensity and the outcome of competitive and facilitative interactions between individual plants (Casper and Jackson, 1997). All these mechanisms interact and affect both plant productivity and the overall nutrient cycling within ecosystems. Understanding how horizontal and vertical heterogeneity of root distribution across time and space affect plant mineral nutrition is therefore essential. We focus here on the horizontal distribution of roots.

An intuitive view is that, in ecosystems limited by belowground resources, the volume of soil explored by individual plants should be higher than in resource-rich systems, thus increasing the size of the pool of belowground resources potentially available for them. This view is backed by empirical data, especially in the case of water (Casper et al., 2003). However, a contrasting pattern is also observed in ecosystems such as savanna and grasslands, where plants seem to limit the horizontal distribution of their roots. For example, in nutrient-limited African savanna, dominant tussock grasses of the *Andropogon* and *Hyparrhenia* genera leave the soil between tufts relatively unexplored (Lata et al., 2000; Abbadie et al., 2006). This pattern is also found elsewhere under other tussock grasses species (Groot et al., 1998) as well as under some shrub and tree species in arid ecosystems (Hartle et al., 2006; Guevara et al., 2009). The pattern of restricted exploration of soil by roots can be explained by distinct, but not mutually exclusive hypotheses. First, the limited exploration of soil can be a mere outcome of low plant productivity, physiological constraints or the costs of root construction (Lynch and Ho, 2005). However, this does not seem to be the case for species such as *Hyparrhenia diplandra* in the humid savanna of Lamto, which has a high productivity despite a limited availability of nutrients (Abbadie et al., 2006) highlighting that other assumptions should be considered. Second, plant rooting patterns may simply reflect the underlying pattern of resource distribution: it is well established that plants preferentially proliferate roots within resource hotspots (Mordelet et al., 1996; Hodge, 2004). The shortcoming of this explanation is that it does not explicitly take into account the feedback of root on soil processes through exudation and inputs of dead root material. Indeed, the production of protons or carbohydrates can trigger or locally inhibit specific microbial activities or can alter on the chemical availability of solutes (Hinsinger et al., 2009). We explore here a third hypothesis that takes into account the feedback between roots and resource availability:

we propose that the concentration of the root system in a small volume of soil can be considered, at least in some cases, as a plant strategy to improve plant nutrient uptake through a better control on nutrient cycling. Our objective is twofold: (i) to assess whether and under which conditions the restriction of soil exploration by plants is beneficial for their nutrient acquisition and (ii) to evaluate the consequences of this potential strategy for ecosystem properties, such as soil nutrient stock or nutrient losses.

To understand the consequences of the way plants explore soil on the control of nutrient cycling, we propose a conceptual representation of the exploration of soil by plants at different scales, as illustrated by Figure 2.1. This approach could be applied to any limiting nutrient for plant growth but we take most of our examples from nitrogen and phosphorus nutrition of plants. The rhizosphere represents the volume of soil directly under the influence of roots; it can be seen as a cylinder of soil surrounding roots, in which nutrients, water and exudate concentrations are modified by the root activity (Hinsinger et al., 2009). Its size and shape depend on the process considered (absorption or exudation) and vary along with the solute considered, the soil water content and the root development (Hinsinger et al., 2009; Raynaud, 2010). Depending on the architecture and extension of the root system, rhizospheres of nearby roots can overlap (Pagès, 2011). At the plant scale, we define the plant zone of influence as the volume of soil in which a plant is able to, and usually does, produce roots. It comprises the plant rhizosphere, but also the soil in which no root is present but could be in a near future or have been in a near past. This concept is inspired by (Casper et al., 2003) whose definition was adapted to our framework. At the population scale, we define soil exploration (x) as the proportion of the soil area contained in plant zones of influence relative to the soil outside the zones of influence. We consider a mono-specific population of plants, whose zones of influence do not overlap, *i.e.* without inter-individual competition for nutrients. This allows us to ignore competition for nutrients between individuals in order to focus on the role of spatial extent of roots on nutrient cycling.

Within this framework, if roots are only considered as absorbing organs, a reduced soil exploration should not be considered as an efficient strategy for two main reasons. First, reducing the plant zone of influence (Figure 2.1) lowers the pool of soil nutrients potentially available for plants. For example, if inputs of nutrients to the ecosystem occur mainly as an homogeneous deposition of mineral nutrients through winds or rain at the landscape scale, reducing the lateral exploration of soil by roots deprives plants of a part of this deposition. Second, smaller distances between the rhizospheres of individual plants would create inter-root competition that increases the cost of nutrient absorption (Ge et al., 2000). However, the exploitation of a nutrient pool

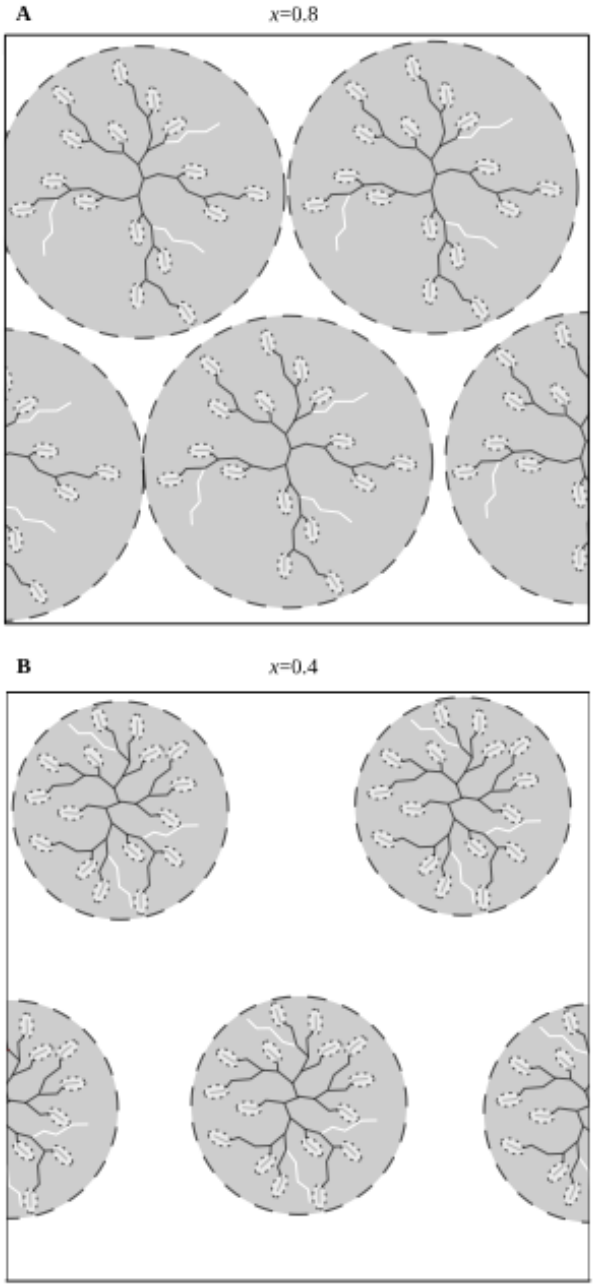

Figure 2.1.: Schematic horizontal maps of the exploration of soil by roots for two plant populations. Black lines correspond to roots that take up nutrients locally in the rhizosphere, shown as white dotted ellipses around apices. White lines denote dead roots. The belowground zone of influence is denoted by grey dashed discs that include all the roots (living and dead) of the individual plants. Soil exploration x is the proportion of soil that is inside the zone of influence relative to total soil. Individuals in A and B have exactly the same quantity of dead and living roots and the same rhizosphere volume. The only difference is that in A the roots are more sparsely distributed than in B. On one hand this results in a lower value of soil exploration x in B than in A. However, on the other hand, rhizospheres in B cover more efficiently the zone of influence and are closer to dead roots, whose nutrients are recycled more efficiently.

often relies on mechanisms others than their mere absorption and these mechanisms may lead to positive effects of the restriction of soil exploration. If an individual plant allocates a constant fraction of its biomass to roots, the restriction of soil exploitation should lead to an increase in its root density, which could in turn increase its capacity to control local nutrient fluxes. This could compensate for the reduced access to nutrients inputs through various processes. In the case of phosphorus limitation, some plants develop "mining" behaviours that couple the exudation of substances that trigger phosphorus availability to the development of "cluster roots" (Lambers et al., 2006). The efficiency of nutrient cycling can also depend on the control of soil microbial activities (activation or inhibition). For example, the biological inhibition of nitrification in tropical savannas is directly correlated to root density (Lata et al., 2000). This process reduces mineral losses through leaching at the ecosystem scale (Boudsocq et al., 2009). Similarly, the rhizosphere priming effect that allows plants to stimulate mineralization within their zone of influence may depend on root density (Shahzad et al., 2012). Once available for absorption, nutrients can be lost for the plant if leached or immobilized by microbial or plant competitors. Reducing the distance of transport from mineralized nutrients to the roots should minimize this risk. A high concentration of roots within the zone of influence should have the same consequence because it increases the probability that a dead root is within the rhizosphere or close to the rhizosphere of a living root (Figure 2.1). Abbadie et al. (Abbadie et al., 1992, 2006) hypothesized that high local concentrations of roots allow nutrients from decaying dead roots to be quickly absorbed by living ones. We thus hypothesize that the existence of functional trade-offs between the area of the soil occupied by plants and the ability of plant to control nutrient cycling within it. To tackle these issues, we developed and analysed two simple models of the cycling of a limiting nutrient using a mathematical framework derived from (Barot et al., 2007) and considering different formulations to describe undocumented trade-offs. In both cases, we only consider the horizontal exploration of the soil in a plant population. In the first model, we consider the proportion of occupied available soil to be fixed (*i.e.* population growth is at equilibrium) and analyse mathematically how this determines variables such as plant biomass, nutrient stock or leaching fluxes. In a second model we added a spatial dynamic of the zones of influence and analyse the consequences of this dynamic on the predictions of the first model.

	Symbol	Meaning/Scale		Unit
Variables	P_O	Plant	In the soil occupied by plants	$kg\ nutrient.ha^{-1}$
	D_O	Detritus	"	"
	N_O	Mineral nutrients	"	"
	D_U	Detritus	In the unoccupied soil	"
	N_U	Mineral nutrients	"	"
	P	Plant	Whole system scale	"
	D	Detritus	"	"
	N	Mineral nutrients	"	"
	T	System total stocks	"	"
	L	Soil total losses	"	$kg\ nutrient.ha^{-1}.yr^{-1}$
Parameters	x	Percent of soil surface occupied by plants		$none$
	r_D	Total input to D compartments		$kg\ nutrient.ha^{-1}.yr^{-1}$
	r_N	Total input to N compartments		"
	l_P,l_D,l_N	Loss rates		yr^{-1}
	u_N	Nutrient uptake efficiency		$ha.kg\ nutrient^{-1}.yr^{-1}$
	d_P	Rate of litter deposition		yr^{-1}
	m_D	Mineralization rate		"
	α_D,α_P,α_N	Recycling coefficients		$none$
	c	Colonization rate (model 2)		yr^{-1}
	μ	Mortality rate (model 2)		"

Table 2.1.: Meaning and units of variables and parameters for the two models.

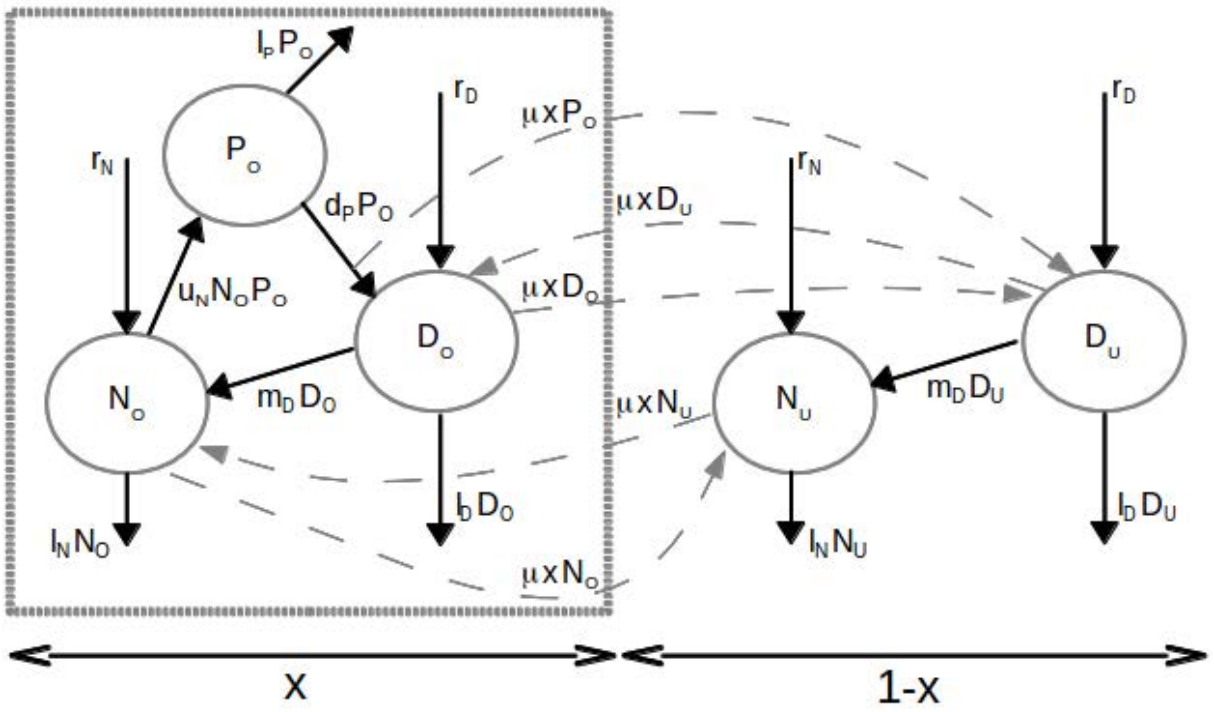

Figure 2.2.: Diagram of the models. We consider nutrient cycling within the soil occupied by plants (within the gray dashed rectangle, subscript O) separately from nutrient-cycling in bare, unoccupied soil (subscript U). The proportion of soil explored is quantified by x (Figure 2.1). Nutrients cycle between 5 compartments : plants (P_O), soil detritus (D_O and D_U and soil mineral nutrients (N_O and N_U). Arrows represent fluxes between nutrient pools within each zone of soil, with their mathematical expression. Plain arrows correspond to fluxes of model 1, while dashed arrows are fluxes added to model 1 to form model 2.

2.3. Material and Methods

2.3.1. Models descriptions

2.3.1.1. Spatial organization of the plant-soil system

For simplicity, we use an implicit representation of space where we divide the soil on the horizontal plane into two distinct areas: the soil that is occupied (O) or unoccupied (U) by roots. This is a discrete approximation of the horizontal distribution of roots, which is generally more continuous in the field (Hook et al., 1994; Lata et al., 2000). We assume that, below a threshold value of root density, most of the soil nutrients are out of reach of the fine root rhizospheres. Neglecting possible spatial heterogeneities, we assume a constant and homogeneous rate of aboveground litter and other nutrient inputs on to the modelled area. Parameter x quantifies soil exploration, defined as the proportion of soil surface occupied by the belowground zone of influence of plants over the total soil area $0 < x \leq 1$ (figures 2.1&2.2).

We consider a population at equilibrium and suppose x to be constant by making the hypothesis that (i) changes in the occupied/unoccupied status of the soil are due to plant demography, and (ii) plant mortality is perfectly compensated by the appearance of new individuals. We can thus consider compartments of the limiting mineral nutrient to be at equilibrium.

2.3.1.2. Compartments of the nutrient cycle

We model the cycling of a limiting nutrient such as nitrogen or phosphorus that are the most likely to be limiting, in areas O and U. The nutrient cycles between plant tissues (P_O), plant detritus in the soil (D_O and D_U) and mineral pools (N_O and N_U), all expressed in $kg\ nutrient.ha^{-1}$. Total nutrient contents per unit of soil surface (P, D, N) at the whole system scale are calculated using weighted averages:

$$P = x\,P_O \tag{2.1}$$

$$D = x\,D_O + (1-x)D_U$$

$$N = x\,N_O + (1-x)N_U$$

We define T as the total stock of nutrients in the system.

$$T = P + D + N \tag{2.2}$$

2.3.1.3. Nutrient fluxes in the plant-soil system

Inputs of nutrients to the ecosystem are uniform over space and time: r_D for detritus and r_N for mineral nutrients. Losses of nutrients from the system can be due to mechanisms such as fire, volatilization, or harvest. We model them as donor-controlled and proportional to the compartment stocks, with coefficients l_P, l_D and l_N (for plants, detritus and mineral nutrient pools, respectively; see equations below). Nutrient cycling includes three processes: (i) uptake of mineral nutrients by plant roots, (ii) plant losses to the detritus pool, and (iii) mineralization of plant detritus into mineral nutrients. Since nutrient uptake depends on both plant root biomass and nutrient availability in the soil, we model it as a donor-receiver controlled flux proportional to P_O and N_O, with constant coefficient u_N (Barot et al., 2007). Fluxes of organic nutrients between the P_O and D_O occur through organ mortality and root exudation, and increase inputs of nutrients to soil detritus. This flux is donor-controlled, with a rate d_P. We do not distinguish the recycling of above- and belowground plant biomass that we suppose to occur over the same spatial area, *i.e.* within the occupied soil. Finally, mineralization describes the flux between detritus (D_O, D_U) and the mineral nutrient pool (N_O, N_U). We assume that these fluxes are donor-controlled with the same rate m_D. For simplicity, we suppose that all the nutrient cycling parameters that do not depend on the plant compartment (r_D, r_N, m_D, l_D, l_N) are the same between zones O and U.

We developed two models, depending on whether the horizontal dynamics of the two zones are taken into account or not.

2.3.1.4. Model without nutrient fluxes between unoccupied and occupied soil

In the first model we neglect all processes leading to an exchange of organic and mineral nutrients between the occupied and unoccupied soil and therefore assume that nutrient cycles within the two zones are independent. Given the different relations detailed above, the equations for this model are:

$$\frac{dP_O}{dt} = u_N\, N_O\, P_O - (d_P + l_P)P_O \tag{2.3}$$

$$\frac{dD_O}{dt} = r_D + d_P\, P_O - (m_D + l_D)D_O$$

$$\frac{dN_O}{dt} = r_N + m_D\, D_O - (u_N\, P_O + l_N)N_O$$

$$\frac{dD_U}{dt} = r_D - (m_D + l_D)D_U$$

$$\frac{dN_U}{dt} = r_N + m_D\, D_U - l_N\, N_U$$

2.3.1.5. Model considering a spatial dynamic of the zones of influence

The second model assumes that as individual plants die the soil that they occupied is converted to unoccupied, and that unoccupied patches can be colonized by new individuals, thus converting unoccupied to occupied soil. From the model perspective, these mechanisms are equivalent to fluxes of nutrients between the occupied and unoccupied zones, which we model by applying Levins (1969) patch model to the first model (fluxes between the two zones are shown by dashed arrows on Figure 2.2 – see Appendix 6.1 for detailed equations). We consider a dynamic equilibrium where the proportion of soil explored remains constant.

Under this hypothesis, the intensity of horizontal fluxes generated by the spatial dynamics is given by a single parameter: the mortality rate μ (Appendix 6.1).

2.3.1.6. The consequences of space exploration on nutrient cycling parameters

The donor-receiver controlled equation describing nutrient uptake in eq. 2.3 simply expresses that the more roots and the more available nutrients, the higher the nutrient uptake. However, the supply of mineral nutrients within the zone of influence also depends on root activity and feedbacks between these activities and soil (see detailed explanation in the introduction) that may directly increase the availability of mineral nutrients (*e.g.* through mineralization or solubilization) or decrease nutrient losses (*e.g.* through the inhibition of nitrification), which increases the long terme nutrient availability (Hinsinger et al., 2009). Given a certain root biomass, the rhizosphere of a plant with a small zone of influence will more completely fill its zone of influence than a plant with a larger zone of influence (Figure 2.1). If nutrient availability depends on exudation (or other root activities whose effect increases with root density), the zone of influence is better exploited in the former case and the supply of mineral nutrient will be higher. We thus suppose that the root-soil feedbacks are stronger when soil exploration is spatially limited. This leads to assume a negative relationship between nutrient uptake rate (u_N) and soil exploration (x). We test the significance of this trade-off by comparing a version of the model with a constant u_N to a version with a linear trade-off:

$$u_N(x) = u_N^1(1 + \beta_{UN}\,(1 - x)) \tag{2.4}$$

where u_N^1 is the rate of nutrient uptake when all the soil is filled by the roots ($x = 1$), and β_{UN} is the "strength" of the trade-off. This relationship is supposed to be true above a threshold value

xmin under which decreasing soil exploration decreases the uptake efficiency due to competition between roots. We show in Appendices 6.2.1 and 6.3.2 that using other mathematical forms of trade-off can lead qualitatively to the same type of results. Similar arguments can be given for the mineralization rate m_D and the losses of mineral nutrients l_N that may depend on the local root density and thus on x (see Appendix D). In the following, all parameters and variables that are function of soil exploration will be notified by adding (x).

2.3.2. Parametrisation

Our model can be applied to any single-nutrient limited system. To compare it with field data, we focused on nitrogen cycling within two systems: (1) Lamto, a tropical, humid African savanna in the Ivory Coast Abbadie et al. (2006), and (2) a British temperate upland pasture (Batey, 1982). Parameter values are given in Appendix 6.2.2. These two ecosystems are representative of many temperate and tropical grasslands and are characterized by contrasting horizontal root distributions. Long-lived tussock grasses are dominant in the savanna of Lamto and have a spatially concentrated root system leaving large parts of the soil unexplored, whereas temperate humid uplands are hypothesized to have an extensive and more uniform exploration of soil.

2.3.3. Partial recycling efficiencies and system closure

We define partial recycling efficiencies α_P, α_D, and $\alpha_N(x)$ that quantify the proportion of fluxes out of a compartment that reaches the next one for P, D and N compartments, respectively (Barot et al., 2007).

$$\alpha_P = \frac{d_P}{d_P + l_P} \tag{2.5}$$

$$\alpha_D = \frac{m_D}{m_D + l_D}$$

$$\alpha_N(x) = \frac{u_N(x)\, P_O}{u_N(x)\, P_O + l_N} \tag{2.6}$$

We define the system closure $C(x)$ as the product of all the partial recycling efficiencies, which can be interpreted as the proportion of nutrients taken by plants that come from the recycling of their own dead material:

$$C(x) = \alpha_P\, \alpha_D\, \alpha_N(x) \tag{2.7}$$

2.4. Results

2.4.1. Equilibrium and stability conditions

Model 1 has only one non-trivial equilibrium (Eq. 2.3):

$$P_O^*(x) = \frac{1}{d_P(1-\alpha_D\alpha_P)}(\alpha_P(r_N + \alpha_D r_D) - \frac{d_P\, l_N}{u_N(x)}) \tag{2.8}$$

$$D_O^*(x) = \frac{\alpha_D}{m_D(1-\alpha_D\alpha_P)}(\alpha_P\, r_N + r_D - \frac{d_P\, l_N}{u_N(x)})$$

$$D_U^* = \frac{\alpha_D\, r_D}{m_D}$$

$$N_U^* = \frac{r_N + \alpha_D\, r_D}{l_N}$$

To avoid a null denominator for $P_O^*(x)$ and $D_O^*(x)$, l_P or l_D must be strictly positive (see equation 2.6). To be biologically relevant, nutrient stocks have to be positive for all compartments. In the case of $P_O^*$and D_O^*, a single condition is needed:

$$R(x) = \frac{\alpha_P\, u_N(x)(r_N + \alpha_D\, r_D)}{d_P\, l_N} > 1 \tag{2.9}$$

Under that condition, all positive equilibria were shown to be stable (Routh-Hurwitz criteria, Appendix 6.3.1). $R(x)$ can be interpreted as the ratio between the in- and out-flux of nutrients if plants were growing in a formerly unoccupied portion of soil at equilibrium. If $R(x) > 1$, the uptake of mineral nutrient is higher than losses from plant biomass so that plant growth is possible.

$$R(x) = \frac{u_N(x)\, N_U^* P_O}{(d_P + l_P)P_O} \tag{2.10}$$

2.4.2. Conditions for which a reduced explorations optimizes plant biomass

We focus here on the equilibrium size of the plant compartment at the system scale $P^*(x)$ and find values of soil exploration x which maximizes this variable. Using relations 2.6 to 2.8, a simple expression can be found for $C(x)$:

$$C(x) = \alpha_P\, \alpha_D \frac{R(x) - 1}{R(x) - \alpha_P\, \alpha_D} \tag{2.11}$$

Which leads to the following expression for $P^*(x)$:

$$P^*(x) = x(r_N + \alpha_D r_D)\frac{C(x)}{1 - C(x)}\frac{1}{\alpha_D d_P} \tag{2.12}$$

The right hand term of Equation 2.12 can be described as a product between two functions

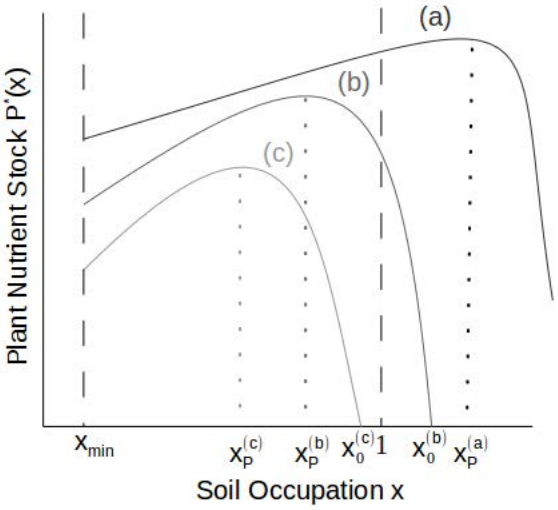

Figure 2.3.: Variation of plant nutrient stock at equilibrium $P^*$with soil exploration x for a linear trade-off. Three different cases are analytically possible: (a) The maximum of the curve is reached for $x_P > 1$. In this case, plant nutrient content is maximized when all the soil is occupied. (b) The maximum is reached for $x_P < 1$, and plant nutrient content is always positive. In this case, the plant can occupy all the space available, but maximizes its mineral nutrition when reducing lateral spread. (c) As in (b) plant biomass is maximized for $x < 1$ but reaches 0 for $x_0 < 1$. In this case, the plant cannot spread over the entire surface available.

of soil exploration. The first is a positive linear function of soil exploration x proportional to nutrient inputs in the mineral compartment of the soil. It expresses the increase in the size of the potentially available nutrient pool with increasing exploration. The second is an increasing function of system closure. It expresses the fact that the more efficient recycling is in the overall system, the higher the plant biomass.

With no trade-off – $u_N(x) = u_N^1$ – the second term of the product is constant and $P^*(x)$ is an increasing function of soil exploration. In this case, plant nutrient stock is always maximized when the plant occupies all the soil available ($x = 1$). Whenever there is a trade-off between nutrient cycling efficiency and soil exploration, biomass at equilibrium $P^*(x)$ becomes the product of increasing (nutrient inputs) and decreasing (nutrient cycling) functions of x (Equations 2.11 &2.12). In that case, $P^*(x)$ has a local maximum for a value of soil exploration (noted x_P).

Figure 2.3 illustrates this variation of P^* with our linear trade-off between x and $u_N(x)$. If $x_P \geq 1$(case (a) on Figure 2.3), plant biomass is maximized when the plant explores all the available space. If $x_P < 1$(situations (b) and (c) on Figure 2.3), plant biomass is optimized when plant exploration is limited. Note that in case (c), P^* becomes negative before $x = 1$, *i.e.* exploration above a given threshold x_0 yields a zero plant biomass. By the use of partial derivation, the analytical expression for optimum soil exploration x_P can be calculated in the

case of the linear trade-off:

$$x_P = \frac{1}{\beta_{UN}}(1 + \beta_{UN} - \sqrt{\frac{1+\beta_{UN}}{R(1)}}) \tag{2.13}$$

A reduced exploration of soil is a beneficial foraging strategy, at least in term of biomass, in cases (b) or (c) of Figure 2.3. In the case of a linear trade-off, this is true whenever:

$$x_P < 1 \;\Leftrightarrow\; R(1) < 1 + \beta_{UN} \tag{2.14}$$

Low values of x_P are favoured by low $R(1)$ ratio and high β_{UN}. According to the definition of $R(x)$(Eq. 9), this is favoured by low mineral nutrient content in the unoccupied soil at equilibrium (N_U^*), which can be due to low inputs of nutrients to the system (r_D and r_N) and low recycling efficiencies alphaD and alphaP, high mineral losses l_N and a high plant mortality $d_P + l_P$. Although being qualitatively similar, other expressions for the trade-off affect the mathematical expression of x_P (Appendix 6.3.2). For a given value of trade-off strength β_{UN}, the model predicts a maximization of plant biomass when a part of the soil is left unexplored at Lamto, whereas in the British pasture biomass is maximized when all the soil is explored (as expressed by the plots of $d_P\ P^*(x)$ on Figure 2.4,panels A and B). The results of the analysis of the first model can be generalized by considering other trade-offs between soil exploration and nutrient cycling parameters: $l_N(x)$ and $m_D(x)$ (Appendices 6.4.1&6.4.2). With these other trade-offs, $P^*(x)$ follows a similarly shaped curve with more complex analytical expressions (Appendices 6.4.1&6.4.2).

2.4.3. Consequences of reduced soil exploration on the plant-soil system functioning

The existence of trade-offs between soil exploration and nutrient cycle parameters (u_N, m_D or l_N) leads to a more efficient recycling of nutrients when soil exploration is reduced. Thus, if there is a strategy of biomass maximization by a limitation of soil exploration (*i.e.* $x_P < 1$), this strategy increases the closure of the system $C(x)$ (Figure 2.3). As a consequence, total nutrient losses at equilibrium, L^*, are minimized (Figure 2.4):

$$L^*(x) = l_D\, D^*(x) + l_N\, N^*(x) = r_D + r_N - l_P\, P^*(x) \tag{2.15}$$

Here we consider the effect of soil exploration x on total mineral (N^*), organic (D^*) and total (T^*) nutrient stocks at equilibrium. D^* is also maximized and N^* is minimized for $x = x_P$

(Appendix 6.3.3). When most of the soil nutrient content is in the organic form, T^* is maximized when $x = x_P$ (Appendix 6.3.4). These results are illustrated in the case of Lamto and the British upland in Figure 2.4.

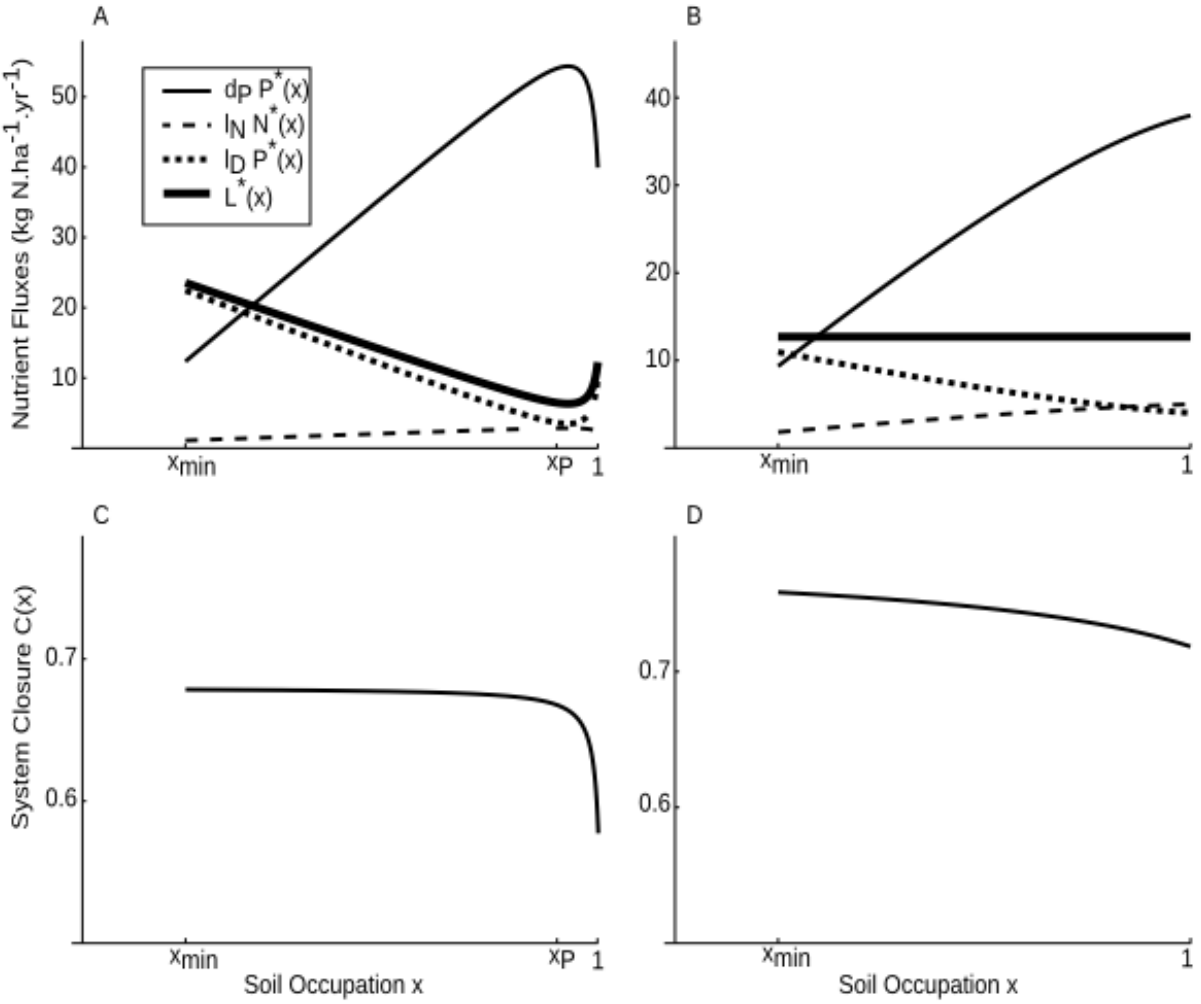

Figure 2.4.: General system properties estimated in the case of Lamto savanna ecosystem (A and C), and a British temperate grassland (B and D) with the linear trade-off and $\beta_{UN} = 1.4$. Panels (a) and (b) show different fluxes as functions of root lateral spread : plant mortality ($d_P P^*(x)$) and soil organic ($l_D D^*(x)$), mineral ($l_N N^*(x)$) and total N losses ($L^*(x)$). Plant mortalities show that Lamto savanna and the British grassland correspond respectively to the cases (b) and (a) described in Figure 2.3. Panels (c) and (d) show the relationship between the system closure C at equilibrium (see Equations 2.7&2.11 for definition) and x.

2.4.4. Role of the spatial dynamics between occupied and unoccupied soil

Our second model is not analytically tractable and no simple general conditions arise for a positive and stable equilibrium. Figure 2.5 was obtained from numerical simulations. Numerical stability was ensured using the Routh-Hurwitz criterion (Appendix 6.1). For the Lamto ecosys-

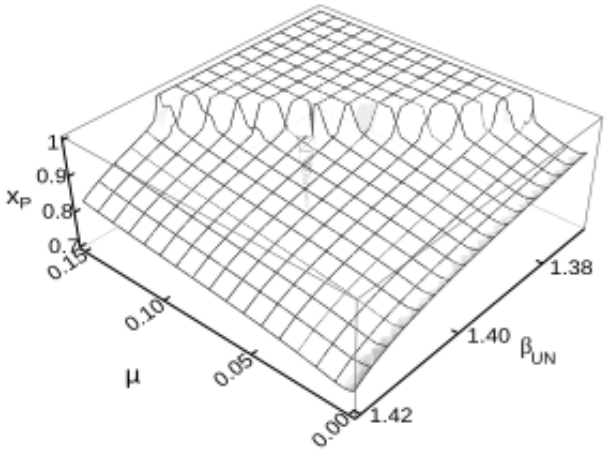

Figure 2.5.: The lateral spread maximizing biomass x_P as a function of lateral fluxes intensity μ and trade-off strength β_{UN}. The Lamto parameter set was used for this figure. Low values of x_P are obtained for low values of mu and high values of β_{UN}.

tem, optimum soil exploration x_P increases with the mortality/colonisation ratio μ and decreases with the trade-off strength β_{UN} (Figure 2.5). This suggests that a restricted exploration would be a less efficient strategy in systems where the plant zone of influence is spatially variable.

2.5. Discussion

2.5.1. When is it beneficial for plants to reduce soil exploration by roots?

Our results can be summarized as follows. Mathematically, restricted soil exploration is beneficial when (1) there is a local maximum for biomass as a function of soil exploration (x), (2) this maximum occurs when soil exploration is lower than 100% ($x_P < 1$) and (3) the spatial dynamics of the area of the occupied soil is low.

Condition (1) is verified when there is a trade-off between exploration and either the nutrient uptake rate or of other components of the nutrient cycle like mineralization (m_D; Appendix 6.4.1) or leaching (l_N; Appendix 6.4.2). The outcome of the model also depends on the strength and the shape of the trade-offs considered. The idea of a trade-off between the size of the foraging area and its control is common in the context of competition (Aikio, 2004), and applies, for example, to the guerilla *vs.* phalanx growth forms of clonal plants (Schmid and Harper, 1985). In this study, we enlarge the scope of this trade-off to plant-soil feedbacks within the belowground zone of influence. Several studies document various nutrient cycling processes, such as mineralization or nitrification that are positively or negatively correlated to root density (Lata et al., 2000; Herman et al., 2006). They support the intuitive idea that sparser root systems control nutrient

cycling less efficiently than denser ones. However, to empirically back our hypothesis of a trade-off between the scale of exploration and the control of nutrient cycling, these observations need to be coupled with estimations of the boundaries of plant zone of influence (Hartle et al., 2006; Casper et al., 2003). To our knowledge, very few studies have quantified both the dimension of the belowground zone of influence of plants together with root density and nutrient fluxes and stocks within it (Lata et al., 2000).

As shown in the introduction, we expect such trade-offs to emerge from the combination of mechanisms of plant-soil feedbacks occurring at small (rhizosphere) or large (zone of influences, total exploration of soil by individuals in a population) spatial scales. Controlled experiments and mechanistic modelling approaches with an explicit representation of space are needed to further explore this hypothesis. At rhizosphere scale, more data are needed to link microbial taxonomic diversity and processes with local root densities and how this impacts the upper scale of the plant zone of influence (Lata et al., 2000). Models inherited from the Barber Cushman approach (*e.g.* Raynaud 2010) should concomitantly help to define which nutrient and under what conditions the augmentation of root density within the zone of influence can lead to (i) positive relations between root density and nutrient uptake efficiency and (ii) negative relations between root density and nutrient losses through leaching and denitrification.

The upscaling to the belowground zone of influence could then be achieved using architectural models of the root system (Pagès, 2011),or continuous root distribution modelling (Dupuy et al., 2010). They should help the analysis of the impact of local changes of root density within the zone of influence on plant control of belowground processes. Feedbacks between plant population dynamics, the exploration of soil and the control of nutrient cycling should be studied to determine under which conditions the spatial dynamics of individuals in a plant population affect the control of plants on nutrient cycling. Finally, the explicit representation of space in mechanistic modelling should allow the study of the consequence of interactions between restricted soil exploration and root foraging strategies of plants subject to competition for heterogeneously-distributed resources.

Condition (2) for a beneficial restriction of soil exploration (Equation 2.14) is verified for low concentrations of mineral nutrients in the unexplored soil N_U^*, which happens when (i) nutrient inputs in the soil are low and/or (ii) soil recycling efficiencies or soil nutrient availability are low, *e.g.* for high leaching rates or high clay content. This condition applies quite well to many wet tropical soils, especially sandy soils, that are very poor in organic matter and are subject to heavy rains (Sanchez and Logan, 1992; Abbadie et al., 2006). It is in contradiction

with the common view that belowground ecosystems limited by soil resources should show a more complete exploration of soil. This contradiction can be solved by distinguishing foraging strategies for water and nutrients. As water is a resource that cannot be recycled within the soil, the main way to increase its access is to explore a larger volume of soil, horizontally or vertically Casper et al. (2003) as in a very arid ecosystem. In contrast, mineral nutrients are partially recycled locally through the production of dead organic matter, within the zone of influence of a plant, so that the availability of mineral nutrients can be improved either by accessing a yet unexploited nutrient pool through an increase in the size of the root system or by a tighter control of the local nutrient cycling to increase the local availability of mineral nutrients.

Finally, from condition (3) for a beneficial restriction of soil exploration, resulting from our second model, the benefit of a restricted exploration increases with the spatial stability of the area of soil explored. Spatial stability is a function of plant life history traits: perennial plants occupy the same volume of soil longer than annual plants that are less susceptible to benefit from the recycling of their own dead roots. However, the spatial stability of soil exploration can also be enhanced over generations by other traits such as low dispersal or nursing effects that favour recruitment of seedlings near the parent plants (Pugnaire et al., 1996). Factors influencing plant mortality, such as fire regimes and herbivory should also affect the spatial stability of soil exploration.

2.5.2. Generality of model predictions

Our model predictions fit quite well with the common observation of heterogeneous belowground vegetation patterns in harsh environments (Abbadie et al., 2006; White, 1970). This is also in line with the fact that territoriality in root foraging, which leads to a horizontal partitioning of root systems within communities (Schenk et al., 1999), is more often observed in harsh environments than in richer ones, where root systems are intermingled (de Kroon et al., 2012). However, this pattern can be due to other constraints such as pre-existing soil heterogeneity (Mordelet et al., 1996) or water limitation (Kéfi et al., 2008).

Besides these harsh *vs.* rich ecosystem considerations, the conditions discussed above as well as our numerical applications suggest that the strategy of limited exploration applies quite well to perennial tussock grasses growing within wet tropical or semi-arid desert soils, or more generally to ecosystems where balanced foraging strategies for water and nutrients are more focused on nutrients. Compared to shrubs and trees, grasses are less able to grow roots at long distance (Schenk et al., 1999) and are thus less likely to benefit from large-scale heterogeneities of soil

resources. However, reduced soil exploration could enhance, amongst others, their ability to control microbial processes such as nitrification inhibition. This is illustrated by some perennials of the Andropogoneae group that invade huge areas in South America or in Australia, where they outcompete native annuals or perennials not having this capacity (Rossiter et al., 2009).

A prediction of our second model is therefore that perennial tussock grasses should be observed more frequently in nutrient-poor ecosystems (Tilman and Wedin, 1991). Note that our three conditions apply to ecosystems where primary production is limited by either nitrogen or phosphorus. At the moment, the N cycle is better documented than the P cycle and future studies may well document mechanisms that link root foraging strategies, root density and fluxes of P, leading to the kind of trade-offs hypothesized here.

2.5.3. Potential applications

In our model, restricted soil exploration not only enhances plant nutrient stock, but also improves nutrient cycling on the whole system scale (nutrient cycle closure $C(x)$). The rate of nutrient loss from soil compartments (L^*) is lowered while soil organic nutrient stock (D^*) is maximized. This is consistent with the common observation of organic matter accumulation under tussock grasses (Derner and Briske, 2001), which are used to increase fertility during fallows (Somé et al., 2006).

Another, more direct, consequence of soil exploration limitation is the creation of a spatial heterogeneity, with patches of soil densely occupied by roots and others left unexplored. A first point that should be discussed in further studies is the contribution of exploration limitation to the creation of islands of fertility, as often observed under perennial plants and tussock grasses (Wezel et al., 2000; Derner and Briske, 2001). A second point is the effect of this heterogeneity on species interactions. On one hand, exploration limitation is *de facto* part of a phalanx strategy: a plant that controls soil processes should be also able to locally outcompete other plants. On the other hand, soil exploration limitation should lead to partitioning of soil exploration between individuals and species, thus limiting competitive interactions at a wider scale (Schenk et al., 1999). In the Lamto savanna, statistical analysis of the spatial distribution of grass tufts showed that they were randomly rather than regularly distributed as would have been expected if competition was strong, thus suggesting that competition between tufts is low (Abbadie et al., 2006). Competition (between either grass or tree populations), that was ignored in our study, should also be taken into account to understand how a limited exploration strategy can be selected at the evolutionary scale. This could be achieved by individual-based and spatially explicit

modelling at the population scale.

In the context of ecosystem resilience to climate change, understanding the balance between plant foraging strategies for water and nutrients and whether it leads to enhanced or reduced soil exploration, should be of great importance. Even if grasses are less able than trees to grow roots over long distances, they have high plasticity in root proliferation. For example, (Schwinning and Ehleringer, 2001) showed that depending on water source (pulse *vs.* deeper soil water) in arid ecosystems, plant could adapt switching from shallow *vs.* deep root systems. Such plant behaviour and associated trade-offs when considering modifications in rain events or soil moisture should therefore impact plant fitness, competition and ecosystem resilience. Finally, in the context of global change, several authors also stress the limits of conventional agriculture in terms of nutrient losses and call for more nutrient-efficient cultures (Tilman, 1999; Weiner, 2004; Subbarao et al., 2013; Malézieux, 2011). One of the ways proposed is the mimicry of natural systems that have higher productivity and lower nutrient losses (Malézieux, 2011). Perennial cultures are particularly interesting considering their capacity to maintain high levels of carbon (Weiner, 2004) or nitrogen (Subbarao et al., 2013) in soils. Some authors have proposed that new varieties of perennial cereals need to be developed (Cox et al., 2006). As suggested by our study, one of the traits that could be selected in these new varieties would be the capacity of plants to control nutrient cycling through restricted soil exploration.

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Perspectives

Cet article a pris le point de vue d'une plante développant une stratégie optimale d'occupation du sol. Le formalisme développé permet également de s'intéresser au fonctionnement global du système plante-sol. Un premier sujet d'étude que j'ai commencé à développer au cours de cette thèse est la question de la formation d'îlots de nutriments. Une stratégie de contrôle local du recyclage des nutriments mène-t-elle systématiquement à l'augmentation locale du pool de nutriments du sol ? Les îlots de nutriments sont-ils une partie intégrante d'une stratégie d'exploration efficace du sol, ou bien un simple effet secondaire d'un patron racinaire hétérogène ?

A plus long terme, un projet de modélisation recherche à reprendre le raisonnement de cet article dans le cadre de modèle individus-centré, avec différentes plantes individuelles avec des niveau d'étalement racinaire différents en compétition. Cette démarche permettrait de faire le lien entré l'échelle individuelle et celle de la population, sur laquelle je me suis concentré dans cet article. Ce type de modélisation permettrait également de mieux prendre en compte le caractère dynamique de l'occupation du sol.

Troisième partie .

Patrons d'exploration racinaire, effet îlot de fertilité et cycle de l'azote chez trois espèces de Poacées pérennes de savane.

Introduction de la partie

Les hypothèses et concepts à l'origine de cette thèse ont été pour beaucoup formulés et paramétrés (*Cf.* chapitre 2) dans le cadre de l'étude de la savane humide de Lamto (Côte d'Ivoire)(Abbadie et al., 2006), où la pression en herbivores est faible et la pluviométrie élevée. En vue de vérifier la portée générale de ces idées, j'ai effectué une campagne de terrain sur la savane semi-aride de Hwange (Zimbabwe), où les grands herbivores sauvages sont présents en très grand nombre, où la pluviométrie est plus basse qu'à Lamto et qui est soumise à de fortes pressions anthropiques et de changement climatique. Le travail de terrain à l'origine de ce chapitre a pour objectif de mettre à l'épreuve du terrain les concepts et hypothèses de cette thèse, et les prévisions du chapitre 2.

Dans le chapitre de synthèse, je soulignais que les Poacées pérennes sont un modèle intéressant afin d'étudier les interactions entre occupation et exploration du sol. Dans l'étude de terrain présentée dans ce chapitre, je me suis concentré sur **trois espèces dominant la strate herbacée** de la savane de Hwange. Mon objectif était de **caractériser leur mode l'exploration du sol** et leur occupation du sol de deux manière : la **formation d'îlots de fertilité** à l'aplomb des touffes d'herbes, ou **l'estimation des flux du cycle de l'azote par l'interprétation de données isotopiques**. J'ai également testé les effets conjugués de la **limitation en nutriments** et de la présence des **grands herbivores** sur le mode d'exploration et d'occupation du sol, par le biais d'une expérience de long terme initiée en 2008.

3. Root exploration pattern and nutrient cycling in the plants-soil system of three savanna grasses

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3.1. Abstract

1. Perennial grasses play an important role in the functioning of many grasslands and savannas, especially through their influence on herbivory and on its fertility through their long-term interaction with soil. They have various growth forms (caespitose *vs.* rhizomatous), degree of palatability and feedbacks on nutrient cycling. In particular, caespitose grasses often lead to the local accumulation of carbon and nutrients ("island of fertility effect") and are sometimes able to control the cycling of nitrogen. Here our aim is to link the root exploration pattern and degree of palatability of different grasses to their ability to influence nutrient cycling.

2. Our main hypotheses is that caespitose grasses have more heterogeneous root exploration pattern than rhizomatous grasses. They should subsequently have a stronger influence on nutrient cycling, by the formation of island of fertility, and a less open nutrient cycle (*i.e.* with less losses). This effect is expected to be stronger for large than for small caespitose. We also consider the role of constraints such as nutrient limitation and the presence of large herbivores. Nutrient limitation should either lead grass to explore a wider area or to invest more in the control of nutrient cycling and have a more localised root system. The presence of large herbivores induces grass consumption, as a function of their palatability and increases nutrient cycling through dung and urine deposition. We expect that in their presence, grass invest less in the control of nutrient cycling and have a more uniform root distribution.

3. We studied three perennial grasses that are locally dominant in the dry savanna of Hwange (Zimbabwe) and differ in both their growth form and in palatability: *Cynodon dactylon*

(rhizomatous, highly palatable), *Heteropogon contortus* (small tufts, palatable) and *Hyparrhenia filipendula* (large tufts with low palatability). In the context of a long term experiment, we assessed the root exploration pattern, soil chemical properties and nutrient cycling under these three grasses with or without NP fertilisation and in the presence or absence of large herbivores. To assess the ability of grass to control nutrient cycling, we tried to detect island of fertility effects, and used natural abundance of nitrogen isotopes as integrators of this cycle.

4. The pattern of soil exploration was more uniform under *C. dactylon* than under caespitose, and more heterogeneous under *H. filipendula* than under *H. contortus*. The presence of large herbivores lead to a more uniform pattern of root distribution under tufts grasses, but only in the absence of fertiliser. No significant island of fertility effect was found in our study. Higher $^{15}N/^{14}N$ ratio were found under *C. dactylon* than in caespitose grasses, and higher values in *H. contortus* than in *H. filipendula*, which suggests that a concentrated root system is associated to a less intense but more closed nitrogen cycle. The presence of large herbivores tends to reduce $^{15}N/^{14}N$ ratio under *C. dactylon*, suggesting a tighter cycling of nitrogen.
5. This field work allows a general discussion of the relationships between the spatial structure and the functioning of plant-soils systems in the savanna of Hwange. It showed a correspondence between the above- and below-ground exploration patterns of perennial grasses. It also suggests a trade-off between more intense but more open nutrient cycles, involving herbivores and uniform root distribution, and a less intense, but more closed nutrient cycle, under caespitose grasses.

keywords: *Cynodon dactylon*; *Heteropogon contortus*; *Hyparrhenia filipendula*; ^{15}N natural abundance; nitrogen cycling; nutrient enrichment; herbivore; savanna

3.2. Introduction

Caespitose grasses – also named tussock or bunch grasses – play an important role in temperate and tropical ecosystems. As perennials, they interact with soil on the long term, often by the accumulation in the soil of organic matter and nutrients (Derner and Briske, 2001; Burke et al., 1998). This property is often exploited in tropical regions for the regeneration of eroded or nutrient-poor soils during fallows (Somé et al., 2006). They are also able to maintain a high

productivity in harsh conditions and dominate many arid or nutrient-poor ecosystems (Coffin and Lauenroth, 1991; Abbadie et al., 2006). As a consequence of these abilities, some grasses became invasive in ecosystems worldwide where they were introduced as food for cattle (Rossiter et al., 2006; Baruch and Bilbao, 1999). In several tropical savannas, they regulate tree demography as main fuel for fires during the dry season (Abbadie et al., 2006). These emergent properties of perennial caespitose grasses, distinct from perennial rhizomatous grasses, could lie in their peculiar horizontal distributions of plant biomass. As above-ground, their below-ground biomass is aggregated on a small surface and within a small volume of soil (Lata et al., 2000; Abbadie et al., 2006; Schenk and Jackson, 2002; Milchunas and Lauenroth, 1989). We therefore considered in this study whether this aggregated soil exploration pattern of caespitose grasses plays a role in their mineral nutrition.

Here, we use "soil exploration" to describe the finite volume of soil circumscribed by plants during the development of their root system and that constraints the overall pool of nutrients potentially accessible to roots. We define "soil occupation" as the ability of plants to influence nutrient cycling within this volume, through *e.g.* exudation or symbiosis (Chapman et al., 2006). We propose that a trade-off between the extent of soil exploration and the efficiency of soil occupation may be involved in the growth form of perennial grasses (chapter 1.5). This idea is somewhat already expressed in the "guerilla" *vs.* "phalanx" metaphor in the context of plant competition (Clegg, 1978; Harper, 1980). Caespitose grasses are a case of phalanx strategy, that minimises soil exploration but confers them a competitive advantage for resource exploitation. Here we consider the consequences of this form of territoriality (Schenk et al., 1999) on nutrient cycling in the soil explored by tufts grasses. In the specific case of tropical caespitose grasses Abbadie et al. (1992, 2006) proposed that the proximity of dead and living roots would favour an efficient recycling of mineral nutrients contained in dead roots. A strong control of microbial activities is also documented in the vicinity of living roots of some tufts grasses (Lata et al., 2004; Armas and Pugnaire, 2011). According to our hypothesis of an exploration/occupation trade-off, we expect that perennial caespitose grasses rely more on a tight control of nutrient cycling than rhizomatous for their mineral nutrition and that the more aggregated their exploration is, the tighter this control.

Constraints such as nutrient limitation and the presence of large herbivores are bound to influence the relationship between soil exploration and soil occupation. Different effect of nutrient limitation should be expected depending on plant nutrient acquisition strategy. A plant that forages efficiently for readily available nutrients should explore a larger soil volume with

increased nutrient limitation, to access a larger pool of nutrients. By analogy, plants of arid ecosystems tend to spread their roots for water access over a larger area than in semi-arid and humid ecosystems (Casper et al., 2003). A plant that invest in nutrient cycling, for example through a "mining" behaviour (Lambers et al., 2008), should invest more in dense and aggregated root systems, and exudation. In this study, we focus on the limitation by phosphorus and nitrogen. Large herbivores, for their part, have diverse effects on grasses that affect nutrient cycling and may affect grass exploration strategies (Huntly, 1995). By definition, grazers consume grasses and thus increase grass demand in nutrients. This effect should be correlated to grass palatability: more palatable grasses have higher concentration in nutrients and are more intensively grazed. All large herbivores (*i.e.* both grazers and browsers (Scholes and Archer, 1997)) redistribute available nutrients through urine and dung. Palatable grasses, by attracting grazers may benefit from this input (de Mazancourt et al., 1998). Urine and dung often boost nutrient fluxes such as mineralization and nitrification (Coetsee et al., 2010; Frank and Evans, 1997) but can also, although not always, increase nitrogen losses by volatilisation (Coetsee et al., 2010; Frank et al., 2000). Trampling also affect soil functioning by inducing compaction, therefore affecting soil water potential and the mobility of inorganic nutrients (Huntly, 1995). Depending on the outcome of both grass consumption and urine and dung deposition, the presence of herbivores should either increase (through increased demand in nutrients and soil losses) or decrease (by increasing the availability of nutrients) the grass nutrient demand, and thus their root exploration behaviour. In general, herbivores should induce more uniform patterns of root exploration (Milchunas and Lauenroth, 1989).

Here we analyse data from the dry savanna of Hwange National Park (Zimbabwe), that is characterized by nutrient-poor, sandy soils and a strong constraint in herbivory (Tafangenyasha and Campbell, 1998; Childes and Walker, 1987). The objective of this field work was to characterize in real-world conditions the exploration patterns for two dominant caespitose grasses and a rhizomatous grass differing in their size and palatability. We assess how their belowground exploration pattern is constrained by nutrient limitation and the presence of large herbivores and how it can be related to grass nutrient strategies. Our work is part of a long term experiment meant to evaluate the interactive effects of herbivores and nutrient limitation (N,P) on vegetation. Soil exploration was estimated by measuring the root horizontal distribution of these species. Soil occupation was estimated by two different methods. First, we compared the carbon and nutrient contents of soil directly under grasses to areas of bare soil, to detect possible "island of fertility" effects *(Vinton and Burke, 1995; Derner and Briske, 2001).* Second, focusing on ni-

trogen, we measured its isotopic composition in plants and soil. Isotopic ratios of nitrogen are often used as integrators of the cycling of this element (Högberg, 1997; Robinson, 2001; Dawson et al., 2002). In plant ecology, variations of plant and soil $^{15}N/^{14}N$ ratios are explained by a wide range of factors including climate (Craine et al., 2009; Amundson et al., 2003), rates of mineralization and nitrification (Templer et al., 2007), plant uptake of different nitrogen sources (Abbadie et al., 1992; Amundson et al., 2003) and association to different types of mycorrhizae (Craine et al., 2009). It is thus a useful tool in the context of our study for getting an overview of the nutrient strategies of our focus grass species and on the intensity of nutrient cycling in the soil they explore.

From this introduction, we formulate the following hypotheses, as a framework to interpret our data:

- H1: Soil exploration is more local for the two caespitose than for the rhizomatous grasses, and more local for bigger tufts than for smaller ones.
- H2: Caespitose grasses lead to a local accumulation of carbon and nutrients (island of fertility effect), correlated to the aggregation of their root biomass.
- H3: Caespitose grasses have a greater influence on nitrogen cycling than rhizomatous grasses, as well as bigger tufts compared to smaller ones. This should be expressed by a gradient of isotopic composition.
- H4: By lowering nutrient limitation, fertilisation should increase the investment of grasses in roots and decrease root aggregation. This should reduce the plant control on nutrient cycling, and thus limit island of fertility effects.
- H5: The presence of herbivores should increases investment in roots for the most palatable grasses. It should lead to more uniform root distributions and limit island of fertility effects. On the contrary, the presence of herbivores should for the most palatable plants increase the investment of grasses in roots, tightening up plant control of nutrient cycling. It should in general lead to more open nitrogen cycles.

3.3. Material and Methods

3.3.1. Study site

The field site is located near the main Camp area of Hwange National Park, in the West of Zimbabwe (26°57'E, 19°16'S, alt. *ca.* 1100 m a.s.l.). The climate is semi-arid with a rainy

Table 3.1.: Summary of the explanatory variables, their abbreviation and signification

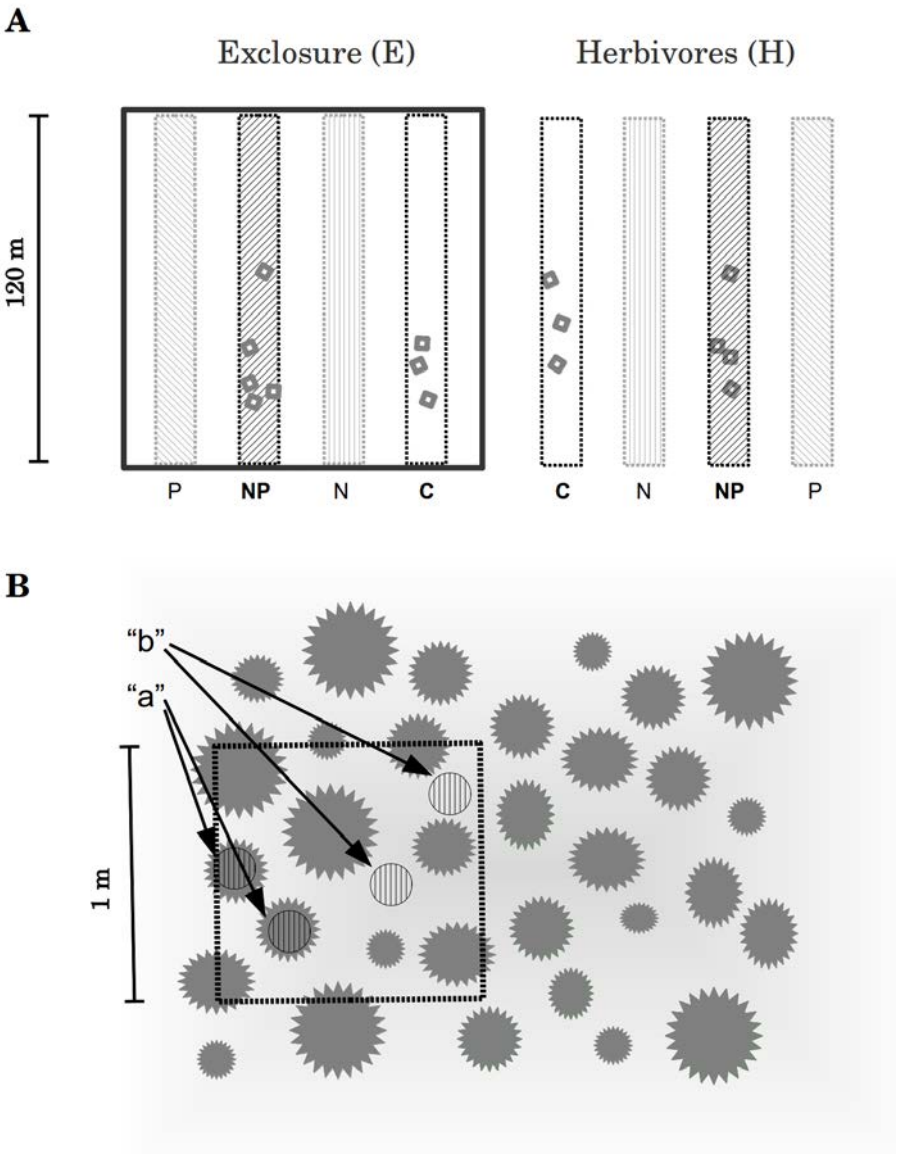
variable	abbreviation	full name/meaning
species	*CYD*	*Cynodon dactylon*
	HEC	*Heteropogon contortus*
	HYF	*Hyparrhenia filipendula*
herbivore	E	within exclosure: no herbivores
	H	outside exclosure: with herbivores
fertilization	C	Control
	NP	N and P added
plant cover	a	under grass cover
	b	under bare soil surface

season lasting from October to April. Mean annual precipitations are *ca.* 606 mm with 25% of inter-annual variability (Chamaillé-Jammes et al., 2006) and mean annual temperature is *ca.* 20.3°C (Childes and Walker, 1987). Hwange National Park is composed of 95% in the Kalahari sands (Childes and Walker, 1987). Soil is sandy and poor in nutrients (Childes and Walker, 1987), and, in the specific area where the study was performed, shallow (ca. 40 cm deep), over a calcareous rocky bed. Vegetation on the study site is a relatively open acacia savanna, with a patchy distribution of dominant perennials (see below). Herbivores present on the site are mainly ungulates and elephants – See (Valeix et al., 2007, 2008) for more details.

3.3.2. Experimental design

In December 2007, two experimental blocks of 120 x 260 m (figure 3.1) were set up to study the long-term effect of the presence/absence of large herbivore and nutrient limitation on plant and soil structure and functioning. Within each block, three treatments were applied in a nested split-plot design. In each block, two areas were defined: inside an exclosure (E – a termite proof fence 2.1 m high to exclude large mammal herbivores), and outside (H – *i.e.* submitted to the activity of herbivores). In each of these areas, four 15 m wide strips of vegetation separated by 20 m wide buffer zones were submitted to different fertilization treatments: control (C), nitrogen (N), phosphorus (P) or both (NP). N was added as 150 kg N.ha^{-1}.year^{-1} urea and P was added as 80 kg P.ha^{-1}.year^{-1}, following standards corn fields in the area. Blocks had been chosen so that there was a gradient in tree density (mainly acacia) on every fertilization strip, from an open area on one end to a dense savanna on the other end (from bottom to top on panel A of figure 3.1). Two applications were done each year during the wet season (December, February). Application was done by manually spreading the granulates in 10x15 m squares (12 per fertilised strip), just after a rain to facilitate dissolution and reduce the risk of leaching. In the case of our

Figure 3.1.: Schematic representation of field experiment and sampling design. Panel A shows one of the two blocks set up in 2008. Half of it is protected from herbivores by an exclosure (E) while the other area is left open (H). Four strips are defined in each of these areas depending on the fertilization treatments: control without fertilizer (C), nitrogen (N), phosphorus (P) or both (NP). Small squares represent quadrats sampled randomly distributed within each strip, where one of the focus species (*CYD*, *HEC* or *HYF*) is located. Panel B details a sampling quadrat for one of the caespitose species (*HEC* or *HYF*). Aerial biomass distribution (dark grey) was mapped and sampled. Soil samples of the 0-10 cm layer were taken under two plant cover treatments: "a" (soil covered by grass) or "b" (bare soil). The organisation of sampling quadrats for *CYD* was the same, except that the aerial biomass was more homogeneously distributed.



field work, we only focused on the C and NP strips within E and H areas, to get the stronger potential effect of fertilisation (figure 3.1). Our samplings were done in the most open areas, so that the effect of trees could be considered as negligible. See table table 3.1 for a summary of the different treatments.

Every year since 2008, during the rainy season, 2 transects were made to determine locally the dominant plant species, measure vegetation maximum height and estimate aboveground biomass by the use of a herbometer (Prache et al., 1989). Based on these data, we chose three perennial grasses that were locally dominant over a significant area within the experimental plots: *Hyparrhenia filipendula* (*HYF*), *Heteropogon contortus* (*HEC*) and *Cynodon dactylon* (*CYD*). These three species can be classified along a gradient of aerial occupation and palatability. *C. dactylon* is a cosmopolitan, highly palatable, rhizomatous grass (van Oudtshoorn, 2012). *H. contortus* and *H. filipendula* are both caespitose and *H. contortus* tufts are smaller and more palatable than *H. filipendula* (van Oudtshoorn, 2012).

3.3.3. Sampling procedure

3.3.3.1. Quadrat selection

The sampling was achieved in the middle of the rainy season, between the 18th and the 28th of February 2013. After a preliminary estimation of tuft size distribution from ~15 randomly chosen 1x1 m quadrats per species, we decided to sample tufts of ca. 20 cm of circumference, that was among the most frequent for both *HEC* and *HYF*.

We selected for each species (3) and each treatment (4) two quadrats were the focus species was dominant. On each of these quadrats, general measurements were made within the four 50x50 cm sub-quadrats: vegetation aboveground biomass using a herbometer (except for *HYF*, which tufts were too tall), vegetation maximum height and soil depth. The amount of litter was estimated on a pseudo-quantitative scale from 1 (no litter) to 4 (thick layer) by four independent observers. Marks of the four observers were averaged to yield the final litter estimation. We also noticed the presence of other grass species and forbs.

Then each tuft was independently sampled and their location and basal circumference was estimated. A precise map of the aboveground cover was made using aerial photographs taken from a height of 2 m to extract the real locations of tufts on the quadrats, together with a rough sketch of the plot numbering every tuft, sampled and measured (basal circumference) independently. The same method was applied to tufts sampled on quadrats dominated by *CYD* and remaining grass biomass of the four 50x50 cm subquadrats was sampled separately. In

all quadrats, forbs were sampled altogether in separate bags. Within each quadrat, 10 young and green leaves of the dominant species for further analysis (See 3.3.4). In the same purpose, approximately the same mass of aboveground litter was sampled uniformly over the quadrat. Total aboveground biomass was oven dried for 48h at *ca.* 60°C for biomass measurement.

3.3.3.2. Roots and soil sampling

For each quadrat, four soil cores 10 cm deep were sampled with a 8 cm diameter auger (Figure 3.1B): two under vegetation cover ("a") and two under a bare soil surface ("b") (Table 3.1). Just after sampling, samples were dried in a dark room and then sift on a 2 mm sieve, to extract roots and remove stones, plant debris and any fauna visible to the naked-eye. Remaining roots were extracted using the electrostatic method of Kuzyakov (Kuzyakov et al., 2001). The advantage of this method is that it is non destructive for the soil and thus allowed having a match between root and soil analyses. Dried roots and soils were transported separately in sealed bags to be analysed in the laboratory in France.

3.3.4. Analyses performed

After extraction, roots were oven dried (2 days at 60°C) and weighed, which allowed the calculation of root mass per unit of soil mass (mr_M) or volume (mr_V). Roots were then scanned using a HP scanjet 8200 adapted with a Delta-T Scan splash cover (Delta-T Devices, Cambridge, United-Kingdom). Resulting images were analysed with imagej (Rasband, 2014) (see section 7.1 in appendix 7) to get estimations of the length of dry root per unit of soil mass (lr_M) or volume (lr_V) and specific root length (length of root per dry mass of root – srl).

Above- (leaf and litter) and below-ground (roots and 5 g of soil) samples were crushed and sieved 400 µm for CHN (%C, %N, C:N) and isotopic spectrometer ($^{15}N/^{14}N$) analysis, using a Flash HT element analyser coupled with a Delta V advantage Thermo Scientific IRMS. As usual, we expressed isotopic data relative to the atmospheric standard:

$$\delta^{15}N = (({}^{15}N/{}^{14}N)_{sample}/({}^{15}N/{}^{14}N)_{standard}) - 1) * 1000 \quad (3.1)$$

CHN measurements of soil will also be done on decarbonated soil (data not yet obtained). For roots and leaves, we also calculated the isotope discrimination between plant and soil – $\Delta^{15}N_{plant-soil} = \delta^{15}N_{plant} - \delta^{15}N_{soil}$, see table 3.2. Remaining uncrushed soil was used for

Table 3.2.: summary of response variables measured or calculated and their units.

scale	response variable	full name/definition	unit
quadrat	bmtot	total aerial biomass	g
	ht.mx	vegetation maximum height	cm
	ht.hm	herbometer height	cm
	soil.dp	soil depth	cm
tuft	circ	tuft circumference	cm
	bm	tuft biomass	g
root sample	mr_M	root mass per unit of soil mass	g roots.kg^{-1}soil
	mr_V	root mass per unit of soil volume	kg roots.m^{-3} soil
	srl	specific root length	m.g^{-1} roots
	lr_M	root length per unit of soil mass	m roots.kg^{-1} soil
	lr_V	root length per unit of soil volume	m roots.m^{-3} soil
soil sample	dens	density	*none*
	pH_{H_2O},pH_{KCl}	pH	*none*
	$[NO_3]$	nitrate concentration	mg.kg^{-1}
	$[NH_4]$	ammonium concentration	mg.kg^{-1}
	$[P]_{tot}$	total phosphorus	mg.kg^{-1}
	$[P]_{assim}$	assimilable phosphorus (Olsen)	mg.kg^{-1}
leaf, litter, root & soil	C_i	% carbon within the sample i	%
	N_i	% nitrogen within the sample i	%
	$C:N_i$	C:N ratio in sample i	%
	$\delta^{15}N_i$	$\delta^{15}N$ in sample i	‰
	$\Delta^{15}N_{i-soil}$	$\delta^{15}N_i - \delta^{15}N_{soil}$	‰

other analyses including: soil density, pH (H_2O and KCl extraction methods), mineral nitrogen (NO_3^-,NH_4^+) and total and assimilable (Olsen) phosphorus concentrations.

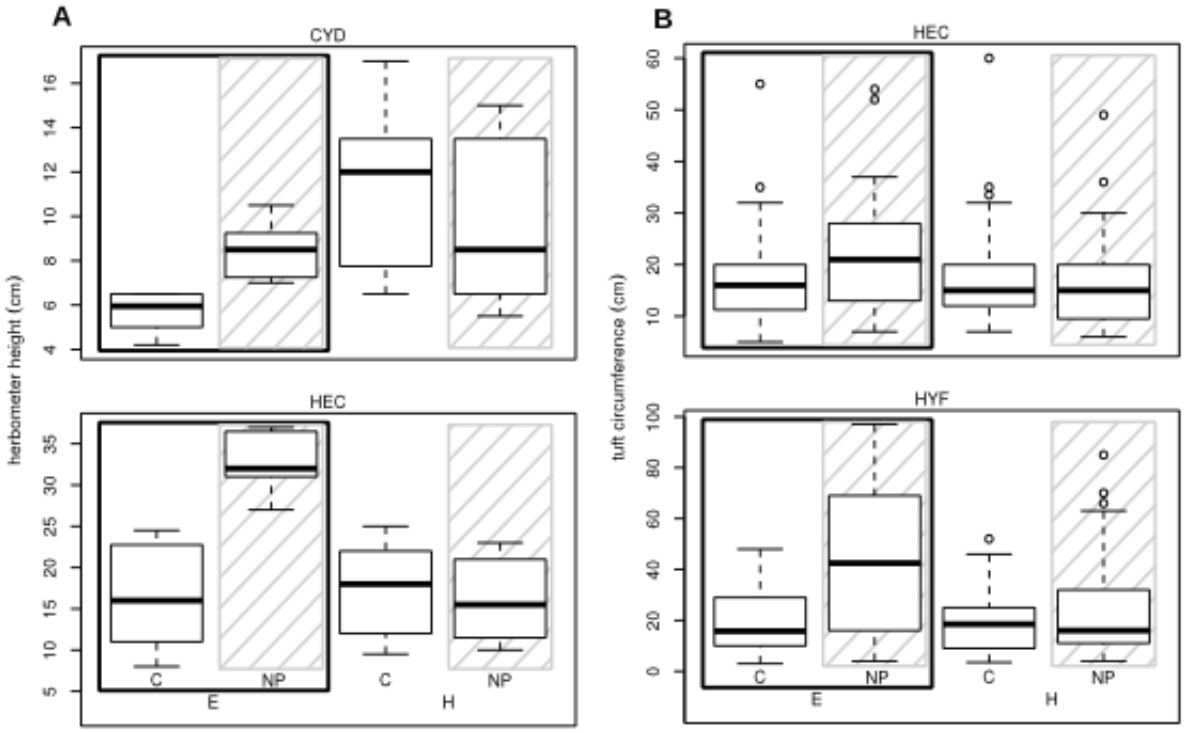
3.3.5. Statistics

We performed our statistical analyses using R version 3.3.1(Team, 2013). Response variables are summarized in table table 3.2. Mixed effect linear models were fitted to the data (nlme package (Pinheiro et al., 2011)). Dominant species, presence/absence of herbivores, fertilization and – when it was needed – soil cover, were used as fixed factors and quadrat within fertilization treatment within herbivore treatment within blocks as random factors. The maximum likelihood (ML) method was used and minimum adequate models were obtained using the stepAIC function (MASS package (Ripley and Venables, 2002)). Tufts biomasses, root mass (mr_V & mr_M) and root length (lr_V&lr_M) variables, soil C and N percentage and total phosphorus content were log-transformed to fit with the anova assumptions. These analyses were also run for each species independently.

3.4. Results

3.4.1. Aboveground biomass pattern

Figure 3.2.: Biomass estimation by herbometer measurements for *CYD* and *HEC* (A) and biomass of individual tufts of *HEC* and *CYD* in the quadrats (B). The exclosure is figured by the black rectangle, and the fertilised strips are figured by a grey, hatched rectangle (See Figure 3.1A).



Total biomass per quadrat differed significantly depending on the dominant species ($F_{14} = 10.8$, $p = 0.0015$) but with no effect of the herbivores and fertilization treatments. There was a gradient of biomass from *HYF* to *CYD* (*HYF*: 1134 ± 162 g.m^{-2}, *HEC*: 637 ± 90 g.m^{-2} and *CYD*: 441 ± 73 g.m^{-2}, expressed as mean $\pm$ s.e.). Although there was no significant interaction between dominant species and herbivore treatment, when analysing data separately for each species, the total biomass of quadrats dominated by *HEC* decreased significantly in the presence of large herbivores ($F_3 = 16.5$, $p = 0.027$).

Herbometer and maximum height measurements (4 per quadrat, See § 3.3.2) as well as data on individual tufts (diameter and biomass) increase the statistical power of models and give an insight into biomass variability within quadrats (Figure 3.2 for herbometer and tufts biomasses). When analysing the data per species, the presence of large herbivores and the addition of fertilisers both significantly increased the estimated *CYD* biomasses compared to unfertilized strip of the exclosure (E C), but these effects were not additive (Figure 3.2A). Overall, *HYF* produced larger tufts than HEC ($circ_{HYF} = 24.8 \pm 1.8$ cm, $circ_{HEC} = 17.6 \pm 0.6$ cm – mean $\pm$ s.e.),

with higher biomasses ($biomass_{HYF} = 81.6 \pm 11.3$ g, $biomass_{HEC} = 21.6 \pm 2.0$ g). Without herbivores (E), *HEC* gave higher herbometer values and produced larger and heavier tufts in the fertilised strip (E NP), but this effect disappeared in the grazed area (Figure 3.2). The same pattern was found for *HYF*, although the heaviest tufts are found in the fertilized strip of the grazed area (H NP – Figure 3.2). Individual tuft circumferences were highly correlated to tuft biomass ($R^2 = 0.77$, $p < 0.001$) as already observed in other African tropical savannas (Lata et al., 2004) and were affected similarly by the different treatments.

3.4.2. Belowground exploration pattern

As for aboveground biomass, there was a significant effect of the dominant species on root mass (mr_M & mr_V) and length (lr_M& lr_V) within the soil sampled (table 7.1 in the appendix), with a gradient from *CYD* to *HYF*: from 0.915 ± 0.06 to 2.79 ± 0.46 g of root per kg of soil (mean ± s.e.), in the case of mr_M.

As expected, *CYD* root distribution tended to be uniform (no significant difference between "a" and "b" cover treatment – figure 3.3). Not surprisingly, caespitose species (*HEC* and *HYF*) root mass (mr_M & mr_V) was higher below tufts than under bare soil (figures 7.3 & 7.4 in the appendix). This pattern was partly due to the presence of thicker, structural roots under the tufts than in bare soil, as reflected by lower specific root length values (figure 7.6 in the appendix). Considering root lengths (lr_M& lr_V – figures 3.3 & 7.5 in the appendix) reduces this bias but leads to the same pattern (table 7.1).

Fertilization and herbivore treatments had no effect as simple factors but fertilization interacted significantly with cover and the dominant species. Both caespitose species tended to have a less heterogeneous exploration pattern (small difference between a and b cover) in the unfertilized strip outside the exclosure (H, C) (figure 3.3). In the case of *HYF* only (figure 3.3, low panel), fertilization lead to higher densities of roots under the tufts both outside (H) and inside (E) the exclosure. Note that under *HYF* and *HEC* tufts, root mass (mr_M & mr_V) and root length (lr_M& lr_V) were positively and significantly correlated to tufts biomasses ($R^2 = 0.45$ to 0.66, $p < 0.01$).

3.4.3. Soil content in C, N and P

Not surprisingly, fertilization had an overall positive effect on soil total and assimilable phosphorus, increasing assimilable phosphorus by 235% and total phosphorus by 42 % (table 7.2

Figure 3.3.: Root length per unit of soil volume (lr_V) in response to herbivore and fertilisation treatments. The exclosure is figured by the black rectangle, and the fertilised strips are figured by a grey, hatched rectangle (See Figure 3.1A). White box figure bare soil and grey box, soils sampled under plants.

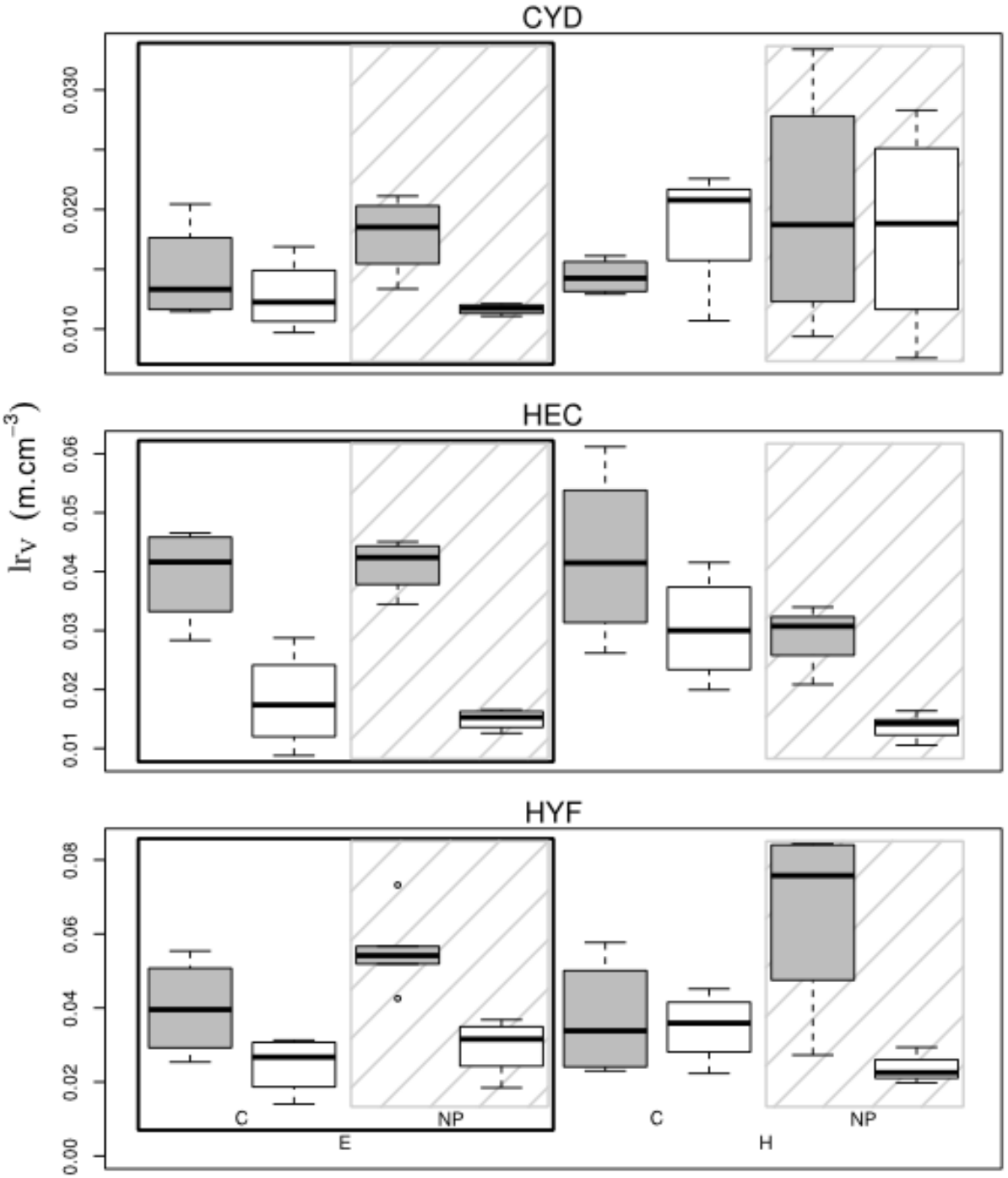


Table 3.3.: Estimate of the effect of grass cover on soil fertility, by comparing carbon and nutrient content (mean ± s.e.) in the soil below grass "a" or bare soil "b" for the three dominant grass species. To avoid the effect of fertilisation, only the unfertilized strips (C) were considered.

sp.dom	cover	% C	% N
CYD	a	1.47 ± 0.11	0.124 ± 0.007
	b	1.10 ± 0.07	0.104 ± 0.005
HEC	a	1.72 ± 0.23	0.116 ± 0.006
	b	1.69 ± 0.27	0.111 ± 0.007
HYF	a	1.28 ± 0.13	0.115 ± 0.009
	b	1.20 ± 0.12	0.107 ± 0.008

sp.dom	cover	$[P]_{tot}$ (mg.kg^{-1})	$[P]_{assim}$ (mg.kg^{-1})
CYD	a	116.6 ± 13.0	8.38 ± 1.64
	b	112.4 ± 15.3	8.50 ± 2.15
HEC	a	112.3 ± 10.8	6.25 ± 1.15
	b	109.9 ± 8.1	5.38 ± 0.96
HYF	a	74.6 ± 5.8	5.57 ± 0.65
	b	79.4 ± 9.3	5.88 ± 0.85

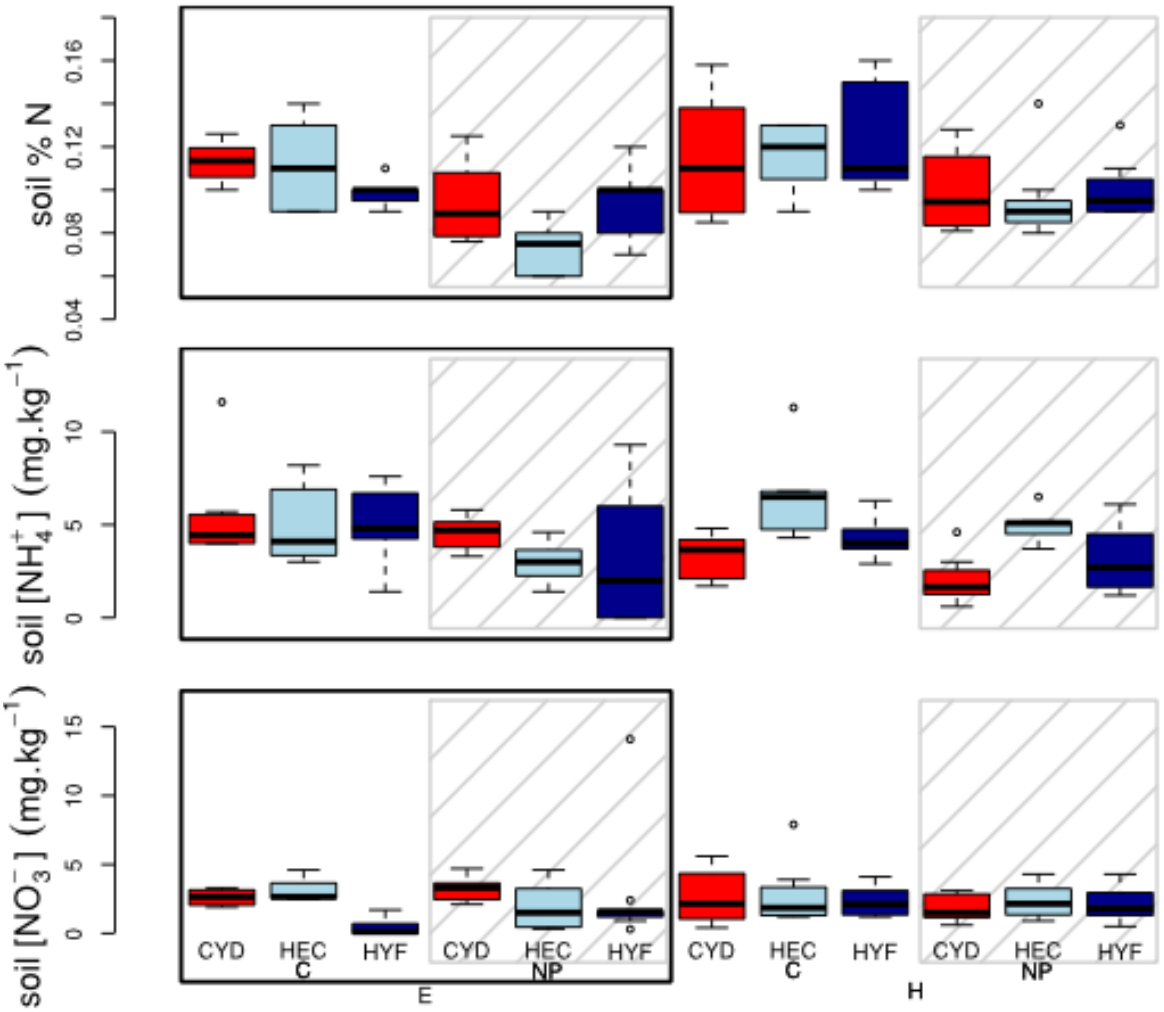
sp.dom	cover	$[NO_3]$ (mg.kg^{-1})	$[NH_4]$ (mg.kg^{-1})
CYD	a	2.84 ± 0.38	4.29 ± 0.24
	b	2.41 ± 0.58	4.46 ± 1.13
HEC	a	2.54 ± 0.47	6.91 ± 0.82
	b	3.33 ± 0.70	4.54 ± 0.48
HYF	a	1.20 ± 0.57	4.49 ± 0.78
	b	1.40 ± 0.46	4.90 ± 0.46

in appendix and figure 3.5). There was also a significant effect of the dominant grass species on these two variables, with a gradient from *HYF* to *CYD* (with a 45% and 49 % increase of mean $[P]_{tot}$ and $[P]_{assim}$, respectively). Fertilisation and herbivore interacted with the effect of dominant species. Differences in soil phosphorus content between the three grasses species were more contrasted in the presence of large herbivores.

Soil % N was significantly and negatively affected by fertilization, with a mean 18% decrease. This may be due to an increased mineralization of soil organic matter in the fertilised strips, as suggested by a decrease of soil % C of the same order of magnitude (22% decrease, with $p = 0.051$). The same pattern was found for ammonium (30% decrease) that, in the presence of large herbivores only, tended to be lower under *HYF* and *CYD* than under *HEC* (figure 3.4).

Grass cover had an overall significant effect on soil % C (+ 9%) and %N (+8%) and on total (+17%) and assimilable (+23%) phosphorus content (table 7.2). However, when analysing the data separately for each species, no significant "island of fertility effect" could be detected (no increase of soil content in carbon and nutrients), except for soil % C under *CYD* and $[P]_{assim}$ under *HEC* (see table 3.3).

Figure 3.4.: Patterns of soil nitrogen content for each of the species in response to herbivore and fertilisation treatments. The exclosure is figured by the black rectangle, and the fertilised strips are figured by a grey, hatched rectangle (See Figure 3.1A). Red box figure the rhizomatous grass (*CYD*) and blue boxes represent the caespitose : *HEC* (light blue) and *HYF* (dark blue).



3.4.4. Nitrogen cycling (plant and soil N stock and δ^{15}N)

Table 3.4 summarises the overall pattern of C, N and $^{15}N/^{14}N$ of soil, plant and litter for our three focus grass species. A significant effect of species was found for all these variables, except in the case of soil C and N content and for leaf δ^{15}N. The stronger pattern was for root N and C:N, with a gradient from *CYD* to *HYF* (- 42% for N and +84% for C:N). This pattern is partly due to the presence of more roots with low specific root length and high C:N under tufts. However, the gradient of root C:N between the three species remained significant when considering separately root sampled under plant (+125 %) or in bare soil (+37%).

A weaker pattern was found for leaves, where *HEC* had low N and consequently much higher C:N than the two other grasses. Aboveground litter followed the same gradient as roots, with increasing nitrogen concentrations from *CYD* to *HYF*. The grass species also had a significant

Figure 3.5.: Patterns of soil carbon and phosphorus content for each of the species in response to herbivore and fertilisation treatments. The exclosure is figured by the black rectangle, and the fertilised strips are figured by a grey, hatched rectangle (See Figure 3.1A). Red box figure the rhizomatous grass (*CYD*) and blue boxes represent the caespitose : *HEC* (light blue) and *HYF* (dark blue).

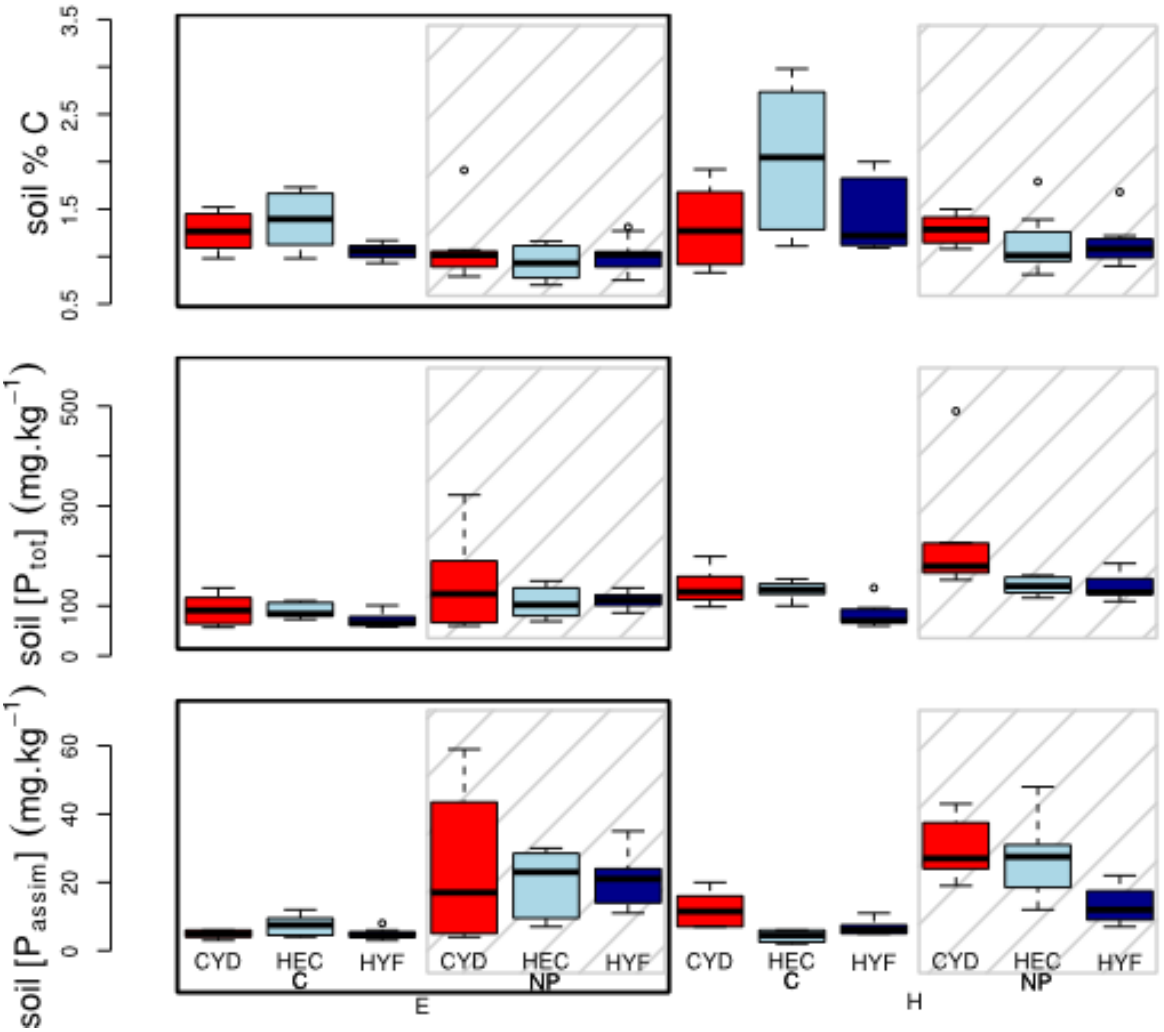


Figure 3.6.: δ^{15}N of soil (panel A) and roots (panel B) in response to herbivore and fertilisation treatments. The exclosure is figured by the black rectangle, and the fertilised strips are figured by a grey, hatched rectangle (See Figure 3.1A).White box figure bare soil and grey box, soils sampled under plants.

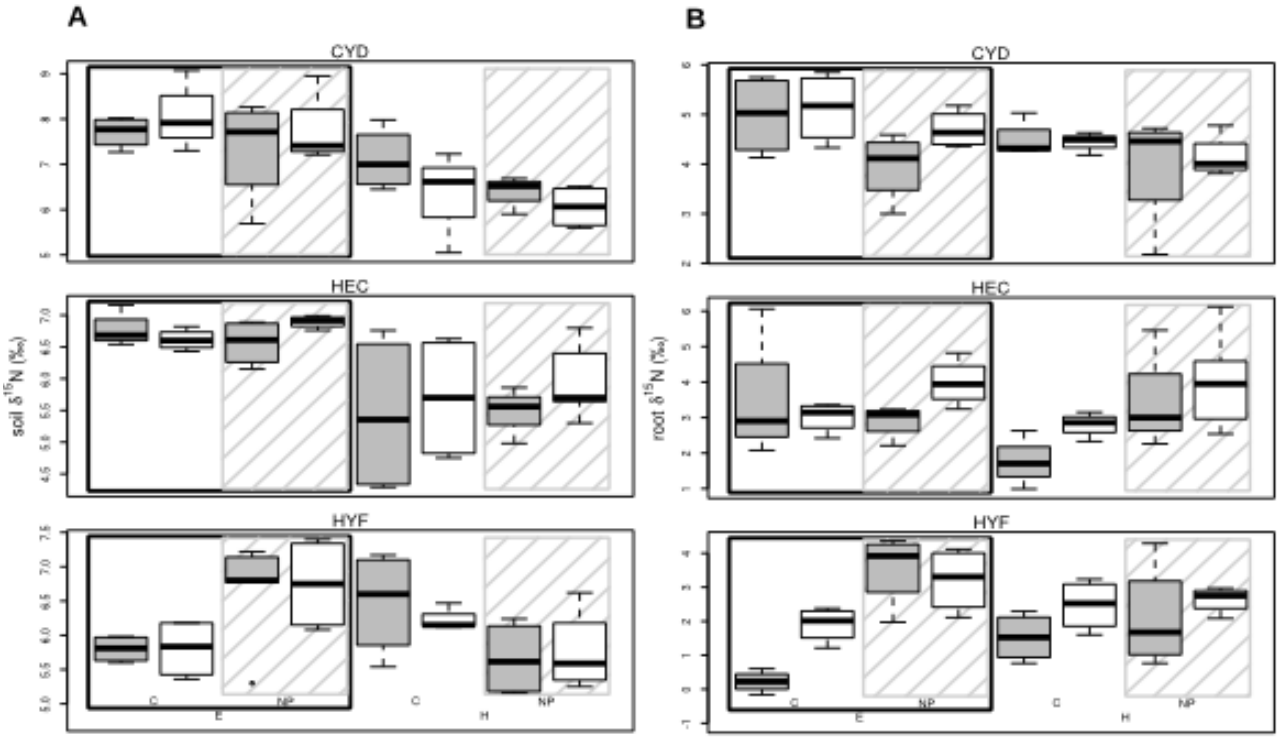


Table 3.4.: C and N and N isotopic content (mean ± s.e.) for soil, roots, litter and leaf for the three species studied. A star denotes a significant effect ($p < 0.05$) of the dominant species as indicated by the ANOVAs.

soil	% C	% N	C:N	δ^{15}N (*)
CYD	1.23 ± 0.05	0.105 ± 0.004	11.7 ± 0.3	7.10 ± 0.17
HEC	1.37 ± 0.11	0.099 ± 0.004	13.6 ± 0.6	6.19 ± 0.14
HYF	1.15 ± 0.05	0.103 ± 0.004	11.0 ± 0.1	6.15 ± 0.11

litter	% C (*)	% N (*)	C:N (*)	δ^{15}N (*)
CYD	38.4 ± 1.6	0.823 ± 0.097	50.1 ± 4.9	2.53 ± 0.24
HEC	35.9 ± 1.1	0.720 ± 0.091	55.9 ± 8.4	1.65 ± 0.87
HYF	36.3 ± 1.3	0.503 ± 0.032	72.4 ± 3.1	-0.35 ± 0.62

roots	% C (*)	% N (*)	C:N (*)	δ^{15}N (*)	$\Delta^{15}N_{root-soil}$ (*)
CYD	35.7 ± 0.9	0.739 ± 0.025	49.9 ± 2.0	4.48 ± 0.13	-2.69 ± 0.14
HEC	33.2 ± 0.9	0.473 ± 0.022	76.1 ± 4.8	3.21 ± 0.21	-2.98 ± 0.22
HYF	36.8 ± 1.0	0.430 ± 0.016	90.9 ± 5.4	2.23 ± 0.21	-3.95 ± 0.17

leaves	% C (*)	% N (*)	C:N (*)	δ^{15}N	$\Delta^{15}N_{leaf-soil}$
CYD	37.3 ± 1.5	1.30 ± 0.08	29.0 ± 1.8	2.90 ± 0.41	-4.20 ± 0.21
HEC	39.5 ± 0.2	1.02 ± 0.04	38.9 ± 1.8	2.21 ± 0.38	-3.99 ± 0.18
HYF	41.0 ± 0.3	1.30 ± 0.06	32.5 ± 0.8	2.47 ± 0.51	-3.65 ± 0.27

effect on δ^{15}N of soil, litter and roots (table 3.4), with a general pattern of increasing δ^{15}N from *HYF* to *CYD*, with the exception of leaves, where δ^{15}N was lower for *HEC* than for *HYF*. The difference of isotopic signature of roots and soil increases from *CYD* to *HYF*. The localisation of the soil sample (a and b cover treatments) significantly affected $\Delta\delta^{15}N_{root-soil}$ as a simple effect and in interactions with the other factors (table 7.4 in the appendix).

Fertilisation, herbivore and cover treatments affected isotopic data in complex ways (figure 3.6 and tables 7.3 & 7.4 in the appendix). When analysing the data for each species separately, fertilisation increased $\delta^{15}N_{leaf}$ of *HYF* and $\delta^{15}N_{litter}$ for both *HYF* and *HEC*. The presence of large herbivores tended to lower soil $\delta^{15}N_{soil}$ in the case of *CYD* ($p = 0.03$). The significant effect of cover on $\delta^{15}N_{root}$ was only found for *HYF* when analysing data per species. This can be linked to differences in root architecture and the fact that HYF is the only of our species to have a significant and positive correlation between its root δ^{15}N and N content ($cor = 0.659$,$p_{value} < 1e-4$)(Högberg, 1997). A positive relationship was found between leaf N and δ^{15}N for *CYD* ($cor = 0.658$,$p_{value} < 1e-4$).

Overall, $\delta^{15}N_{leaf}$ was positively correlated to $\Delta^{15}N_{leaf-soil}(cor = 0.71, p < 1e{-}4)$ and $\delta^{15}N_{soil}$ ($cor = 0.324, p = 0.0016$). The same pattern was observed for roots ($cor(\Delta^{15}N_{root-soil}, \delta^{15}N_{root}) = 0.766$ and $cor(\delta^{15}N_{soil}, \delta^{15}N_{root}) = 0.596$, with both $p < 1e-4$).

3.5. Discussion

Our data on plant biomass and soil nutrient content allow us to draw some general properties of the vegetation in our study site. First of all, estimated biomass and tufts sizes suggest that the growth of grasses is limited by mineral nutrients (N and/or P). NP fertilisation treatment lead to an increase of soil phosphorus content, but a decreased soil organic content. This suggests higher mineralisation rates in the fertilized strips (Chantigny et al., 1999), due to plant-induced priming (Paterson et al., 2008). Higher mineralisation rates in fertilised strips may lead to higher nitrogen availability, but this was not confirmed by the mineral nitrogen concentrations.

The effect of herbivores depended on the grass species, as expected by the gradient of palatability from *CYD* to *HYF*. *CYD* was the only grass that had higher biomass outside than inside the exclosure. This can be interpreted by the fact that the presence of herbivores induces a higher productivity that compensate grass consumption. The fact that the less palatable grasses have higher biomass can be interpreted by the absence of consumption by herbivores, but this effect remains in the exclosure. A second, more probable hypothesis is a lower turnover of biomass

and a long term accumulation of biomass. Some caespitose grasses can indeed have a lifespan of several decades (Garnier and Dajoz, 2001).

Herbivores and fertilisation treatments are known to affect plant communities at a wide range of scales for both their functioning, diversity (Olff and Ritchie, 1998) and demography. These effects are not assessed directly in our study for this time period. Here the focus was on the interaction with the soil of individual tufts of given species, within a same range of sizes (or equivalent surface of soil for *CYD*). The comparison of soil sampled beneath grasses and within close zones of bare soil gives an estimation of the maximum range of plant-soil interactions from minimum (under bare soil) to maximum (under vegetation).

3.5.1. Plant soil exploration strategies

The range of root biomass and length densities is lower and narrower under rhizomatous grass species (*CYD*) than under the two caespitose ones (*HEC* and *HYF*). Moreover, higher root densities were reached under *HYF* than under *HEC*, as for aboveground biomass. Our first hypothesis (H1) is thus confirmed. This pattern was associated with differences of root properties: lower specific root length below tufts, which is associated to higher C:N (Gordon and Jackson, 2000). There are two ways to understand the difference of root densities below caespitose and rhizomatous grass. First, it results from structural constraints: there are more roots with high C:N and low specific root length below tufts, that should interact less with soil than fine roots (Eissenstat and Yanai, 1997). Second, there may be differences in root demography between the different grass species: caespitose grass have coarser roots (Roumet et al., 2006) that are generally longer lived than fine ones (Eissenstat and Yanai, 1997; Gill and Jackson, 2000). As a consequence, as for aboveground biomass, high root densities below caespitose may be the consequence of long-term accumulation of roots within the soil, as suggested by the correlation between tuft size and root density. We can expect root soil interactions at a much longer time-scale for *HYF* than for *HEC*, and for *HEC* than for *CYD*.

Root lengths and biomass densities in bare soil were comparable for the three species. This means that caespitose grasses do not necessarily grow fewer roots in bare soil than *CYD*, but rather that they concentrate most of their belowground biomass under tufts (Lata et al., 2000). The only exception was in the grazed, unfertilized strip, where roots seem to be more uniformly distributed. There was clearly a higher exploration of bare soil in *HEC* quadrats. This pattern may be due to nutrient redistribution by herbivores or higher investment in roots due to grazing. This would be in-line with differences of root pattern inside and outside the exclosures (Milchunas

and Lauenroth, 1989) and partly confirms our hypothesis H5 (herbivores increase investment of the more palatable in more homogeneous root distribution but without effect on island of fertility effect – see below). It is not clear why this pattern did not occur in the fertilised strip outside the exclosure but is likely to be linked to heterogeneity of nutrient distribution. More generally, the fact that fertilisation increased root concentrations below tufts, but not in bare soil is in contradiction with H4 (we expected rather a more uniform exploration pattern in fertilised strips. One can hypothesize that fertilisation increases productivity and thus root growth, but the fact that nutrients are more available reduces horizontal exploration.

3.5.2. Absence of island of fertility effect ?

Our hypotheses on island of fertility effects (H2, H4 & H5) were not verified, as no difference of soil content in carbon and nutrient between bare soil and soil under grasses was observed for our three species, despite the overall effect of cover treatment. This result is surprising since caespitose grasses commonly accumulate C and nutrients in the soil below their tufts (Derner et al., 1997; Derner and Briske, 2001; Vinton and Burke, 1995). The presence of carbonates in soil may affect the pattern of observed C (data on decarbonated soil still to be obtained). Note also that mineral nitrogen data are less representative of long term effect of plants on soil than soil N %, density and P concentrations, being often submitted to temporal variations. However, our hypothesis on island of fertility could also be applied to patterns of nutrient fluxes – instead of stocks as measured here –, such as mineralisation (Vinton and Burke, 1995) or nitrification (Lata et al., 2000). For example, we should expect a more efficient inhibition of nitrification (BNI – (Subbarao et al., 2006)) under large caespitose (Lata et al., 2000) (see paragraph 3.5.3 below).

Although we did not detect long term accumulation of nutrients under tufts at the scale of the quadrat, there was a significant effect of the dominant species on soil phosphorus content. Soil was richer in phosphorus under *CYD* than under *HYF*. This pattern may be either due to the fact that *HYF* depleted phosphorus within soil or that the strategy of soil exploration of caespitose allow them to forage more efficiently for phosphorus when this element is less available. Both hypotheses suggest a "mining" behaviour of caespitose grasses .

3.5.3. Species effects on nitrogen cycling

Our isotopic data are consistent with the global patterns of $\delta^{15}N_{soil}$, $\delta^{15}N_{leaf}$ and $\Delta^{15}N_{plant-soil}$ in the literature (Craine et al., 2009; Amundson et al., 2003). $\Delta^{15}N_{leaf-soil}$ and $\Delta^{15}N_{root-soil}$ were always negative, which is consistent with the general pattern of lower $\delta^{15}N$ in plants than in the soil due to fractionation during plant acquisition of nutrients from soil organic matter (Högberg, 1997).

The factor that impacts the most strongly the isotope signatures is the grass species: the δ^{15}N is higher for the two caespitose species than for *CYD*, and higher in *HYF* than in *HEC*. This is consistent with the difference of isotopic signatures between grazing lawn and adjacent tall grass areas (Coetsee et al., 2010). The fact that this pattern remains even in the absence of herbivores suggests that differences of plant properties such as leaf and litter C:N plays are the most important factors driving δ^{15}N signatures. Lower C:N of plant and litter in *CYD* than in *HEC* and *HYF* suggest that rhizomatous induce a faster nitrogen cycle than caespitose. Field studies correlating δ^{15}N and $\Delta\delta^{15}N_{plant-soil}$ to rates of mineralisation and nitrification (Kahmen et al., 2008) observe that these fluxes are higher under rhizomatous than under caespitose, but this hypothesis should be confirmed by *in situ* measurement of nitrification of mineralisation potential in our study site. Part of the difference of fractionation between our three species could also be explained by differences in nutrient cycling strategies, *e.g.* if caespitose actively inhibit nitrification and have a preference for ammonium over nitrate (Lata et al., 2004). If this hypothesis is true, we should expect a gradient of nitrification rate around tufts, as a function of root density (Lata et al., 2000). The presence of mycorhizal associations also leads to lower δ^{15}N (Craine et al., 2009). Finally, two kind of strategies arise from our data: a fast nitrogen cycling under *CYD* and a slower but potentially more nutrient-conservative cycling under caespitose.

The herbivore treatment also affected soil δ^{15}N, especially for the more palatable grass species (*CYD* and *HEC*). The presence of large herbivores tended to decrease $\delta^{15}N_{soil}$, although the inverse pattern is more common, as herbivores tend to accelerate nutrient cycling (Frank and Evans, 1997; Frank et al., 2000; Coetsee et al., 2010). The fact that herbivores can lower soil δ^{15}N has already been described, but remains difficult to interpret (Xu et al., 2010). An important issue here is to know whether the presence of herbivores leads to a more open nutrient cycle or if they increase nutrient cycling intensity without increasing losses (Frank et al., 2000). Any way, this result suggest that herbivores promote here a tighter nitrogen cycling.

3.5.4. Conclusion

The three grass species studied in this field work can be put along a gradient of root exploration. At one extreme, the rhizomatous grass, *C. dactylon*, had a relatively uniform root exploration pattern with a majority of fine roots that should allow a large surface of interaction with soil but at shorter term (Eissenstat and Yanai, 1997). Caespitose grasses had, in turn, a more heterogeneous exploration pattern, with coarser roots, and *H. filipendula* had a stronger pattern than *H. contortus*. This pattern of root exploration can be related to nutrient strategies in two ways. Our results on phosphorus suggest that caespitose species exploit more efficiently phosphorus. The characterisation of nitrogen cycling suggest a faster but less open cycling below *C. dactylon*, while caespitose grasses should favour a slower, but more conservative nitrogen cycle. It suggests that caespitose of Hwange are able to control nitrogen cycling, for example by the biological inhibition of nitrification (Lata et al., 2004; Subbarao et al., 2006), which raises interesting questions in terms of competition between caespitose and rhizomatous grasses at long-term. To conclude, this study did not really confirm the existence of an exploration/occupation trade-off, but exploration strategies associated to different nitrogen strategies: either a fast or a slow, actively controlled and potentially less open, nitrogen cycling.

The effect of fertilisation and the presence of large herbivores on nutrient cycling and on root exploration pattern and nutrient cycling were more difficult to interpret. The fact that herbivores accelerate nutrient cycling (Coetsee et al., 2010; Frank et al., 2000) and that caespitose are bound to inhibit nitrification raises the issue of the impact of herbivore pressure on the ability of grass to control nitrogen cycling. The answer to this question may help to predict evolution of soil fertility in the savanna of Hwange.

3.6. Acknowledgement

We thank the Director General of the Hwange National Park and the CNRS-LTER Team for providing the opportunity to carry out this research. We thank all the students who helped during the sampling: Nobuhle Ndolvu, Cyntia Mapendere, Gugulethu Mashingaize, Buhlebenkosi Mpofu, Tommy Gaillard. We also thank the rangers of Hwange National Park: Simeon Mudimba Bloomer Mafuwa, Juliet Banda, Philani Dladla. Analytical data were obtained on the ALYSES facility (IRD-UPMC, that was supported by grants from Région Ile de France) and LAMA laboratory (IRD, Dakar). This study was financed by the ANR BIOFUN and SAVARID projects.

Perspectives

Les données générales de la végétation sur l'ensemble du dispositif expérimental peuvent être exploitées à moyen terme pour mieux contextualiser nos données. Chaque année, deux transects par bande ont été effectués au cours de la saison humide, afin d'estimer la distribution des espèces de la strate herbacée et leur biomasse. Ces données permettraient de déterminer de manière plus générale les effets de la présence de grands herbivores sur les biomasses aériennes des différentes espèces, et de découpler les effets des fertilisations à l'azote et au phosphore. Elles permettraient également de mieux comprendre nos données dans un cadre dynamique, sur la durée de l'expérimentation.

Des mesures sur les isotopes du carbone $\delta^{13}C$ ont été obtenus sur les échantillons de sol et de plantes simultanément à celle de $\delta^{15}N$ et sont en cours d'analyse statistique. Ces données peuvent être exploitées de deux manières. Tout d'abord, elles permettraient de discerner dans la biomasse racinaire totale les parties provenant des herbes C3 ou des C4 (dicotydédones herbacées et éventuellement les arbres voisins) (Fry, 2006) et ainsi élargir l'interprétation des données à l'échelle de la communauté. Le $\delta^{13}C$ est également un indicateur de la contrainte en eau, qui est importante sur le site de Hwange (Swap et al., 2004; Wang et al., 2010). On peut émettre l'hypothèse que la forme des touffes cespiteuses leur permet une meilleure résistance au stress hydrique.

En plus des échantillons de sols utilisés dans cette étude, 16 échantillons de sols de 2.4 cm de diamètre et de 10 cm de profondeur ont été prélevés par quadrats, selon une distribution régulière. La mesure de densités racinaires dans ces échantillons permettront une mesure plus complète du degré d'hétérogénéité d'exploration du sol selon l'espèce dominante. Ces données pourront être reliées aux cartographies de biomasse aérienne, notamment pour déterminer les patrons de biomasse racinaire en fonction de la distance aux touffes voisines.

Comme évoqué dans le manuscrit, des données sur sol décarbonaté, qui seront très prochainement acquises, permettront de confirmer ou d'infirmer les patrons de carbone sous la végétation.Enfin, même en l'absence d'îlots de fertilité en termes de stock de carbone et de nutriments, nos résultats isotopiques suggèrent des hétérogénéités de flux de nutriments, qui seront bientôt mesurées par des patrons de minéralisation ou de nitrification (Lata et al., 2000; Coetsee et al., 2010; Xu et al., 2010; Frank and Evans, 1997).

Quatrième partie .

Modélisation de l'impact de la distribution racinaire sur le contrôle du recyclage des nutriments à l'échelle de la rhizosphère et de la zone d'influence souterraine

Introduction de la partie

Les deux approches méthodologiques développées dans les chapitres précédents intégraient un grand nombre d'interactions plantes-sol à l'échelle de la zone d'influence souterraine. Dans ce chapitre, j'adopte une approche mécaniste, en me concentrant sur les interactions directes et localisées des racines vivantes avec le sol. Je me place donc à l'échelle de la rhizosphère, avec pour objectif de tester la première hypothèse formulée dans le chapitre d'introduction : **l'existence possible d'interactions positives entre les racines d'une même plante**. Dans un modèle numérique, je prends en compte explicitement l'exsudation, l'absorption et la diffusion des solutés du sol dans une portion de sol exploré par une plante. En particulier, je considère une plante absorbant du phosphore, dont elle favorise la disponibilité par l'exsudation de citrate. Alors que le modèle mathématique du chapitre 2 intégrait le recyclage des nutriments à l'échelle d'une population de plantes, je teste donc ici ce qui se passe à l'échelle d'une plante unique, entre ses racines. Je teste également l'**hypothèse d'un compromis entre occupation et exploration à l'échelle de la zone d'influence souterraine**.

4. Modelling the impact of root distribution on the control of nutrient availability at the rhizosphere scale: a mechanistic approach

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4.1. Abstract

1. Two complementary root activities are involved in the acquisition of mineral nutrient by plants: nutrient uptake and the exudation of substances that increase nutrient availability. A root interact with soil in a finite volume called the rhizosphere, whose size depend on soil properties such as soil water content but also on the process considered. The overlap of nutrient depletion rhizosphere leads to decreased nutrient uptake efficiency and competition between the roots of a plant but little is known on the consequences of overlap of exudation rhizospheres. Here we test the hypothesis that the combination of the exudation and nutrient depletion rhizosphere may lead to synergies between the roots of a plant.

2. In this study, we use a model simulating plant-soil interactions at the scale of rhizospheres, in the case of a plant absorbing phosphorus, whose availability is controlled by the exudation of a chemical factor. Our aim is to determine if there are conditions leading to positive interactions between roots, expressed as positive relations between root density and nutrient uptake efficiency. In a second step, we scale up root-soil interactions to the whole root system, to assess how the extent of the root system and the distribution of root affect plant mineral nutrition.

3. Our model predicts that positive interactions between roots exist under the conditions of low soil water content and exudation rates, and high nutrient losses by leaching or absorption by microbial competitors. The precise measurement of rhizospheres At the plant scale, our results suggest a trade-off between the volume of soil explored, and the efficiency of the occupation of this volume, defined as the ability of plants to increase

nutrient availability.

4. Our study shows that taking into account the diversity of root functions roots leads to a wider panel of root interactions than mere competition. The possibility of facilitation between the roots of a plant renews our understanding of root foraging strategies.

keywords: root foraging strategies; exudation; rhizosphere; Barber Cushman approach, Phosphorus; nutrient uptake; nutrient availability; soil-root feedback.

4.2. Introduction

Root contribution to plant mineral nutrition relies on complementary processes, nutrient absorption and exudation. On the one hand, plants adjust the location, surface and uptake efficiency of their roots to the local concentration in available nutrients (Hodge, 2004; Mordelet et al., 1996). On the other hand, they are able to locally increase the availability of mineral nutrients by releasing various elements (protons, carbohydrates, secondary metabolites) in the soil surrounding their roots (Dakora and Phillips, 2002). For example, local modifications of soil pH induced by roots alter the solubilization of nutrients such as phosphorus (Hinsinger, 2001). Carbohydrates can boost microbial activities such as mineralization, which can increase local nutrient availability (Kuzyakov, 2002; Fontaine et al., 2003). Secondary metabolites can inhibit other activities such as nitrification (Subbarao et al., 2006; Lata et al., 2004), that indirectly affect the availability of nitrogen (Boudsocq et al., 2009). Many theoretical studies on root foraging strategies have explored how root distribution affected the quantity of nutrients absorbed by plants, depending on the heterogeneity in nutrient distribution (Gleeson and Fry, 1997) and/or the presence of plant competitors (Rubio et al., 2001; Gersani et al., 2001; Robinson et al., 1999). However, relatively few have looked at how the combination of root absorption and exudation could affect the efficiency of plant mineral nutrition (Raynaud et al., 2008).

The main goal of this study is thus to assess the consequence of considering both root absorption and exudation in order to understand the efficiency of a given root exploration pattern on plant mineral nutrition. The development and the activity of the root system are not only ways by which plant explores the soil volume and has access to new pools of nutrients but that also allows them to influence nutrient cycling and to control nutrient availability. We define soil exploration as the fact that, during the development of its root system, a plant circumscribes a finite volume of soil, called its below-ground zone of influence (Casper et al., 2003). We define soil

occupation as the ability of a plant to control nutrient cycling within this volume. This control can imply an increase of nutrient availability, but also a change in nutrient cycling efficiency. This efficiency measures the quantity nutrients made available by root exudates of a plant not lost due to leaching or uptake by other plants or microbial competitors. We use soil exploration and occupation as two complementary concepts to describe root foraging strategies at two distinct scales: the rhizosphere (Hinsinger et al., 2009) and the belowground zone of influence (Casper et al., 2003).

The rhizosphere is the volume of soil directly influenced by living roots, as opposed to bulk soil (Hinsinger et al., 2009). Root absorption and exudation depend on the diffusion and mass flow of the solutes involved (mineral nutrients, root exudates) within the soil solution. Individual roots take up nutrients and release exudates that diffuse at a distance of a few millimetres from their surface (Tinker and Nye, 2000). The size of the rhizosphere depends on the diffusive ability of the solute involved (mineral nutrients or exudates) and on the process (exudation or depletion) considered (Hinsinger et al., 2009; Raynaud, 2010). This has important implications for root foraging strategies. Some authors have applied the concept of competition to the roots of an individual plant when an increase in root density reduced their mean uptake efficiency (the quantity of nutrients absorbed per unit of root length) (Ge et al., 2000). This can be interpreted in term of overlap between depletion rhizospheres (Pagès, 2011): when two roots taking up nutrients are close to each other, they can have access to lower nutrient concentrations than if they were more distant. However, the different size of exudation and depletion rhizospheres could also create synergies between the roots of an individual plant. For example, if root exudation increases the availability of a mineral nutrient in a volume larger than the volume where root can deplete it, the increased availability of nutrients may benefit to neighbouring roots (Raynaud et al., 2008). In such a case, nutrient availability (and so soil occupation) should increase with root density. We thus hypothesize that, under conditions to be determined, the combination of exudation and absorption may lead to facilitative interaction between individual roots within the root system of a plant.

To assess the efficiency of a root foraging strategy, one needs to scale up mechanisms studied at the rhizosphere scale to the scale of the root system (the belowground zone of influence, ZOI). The ZOI is defined as the area over which a plant alter its environment [lien chapitre1]. Its size quantifies soil exploration determine the total pool of nutrient a plant can potentially access, while the distribution of the total root length of the root system should determine the overall soil occupation. When soil occupation increases with local root length densities, as hypothesized here-

above, we expect a trade-off between soil exploration and soil occupation; large volumes of soil cannot be explored with a high density of roots everywhere. We thus also propose the hypothesis of a trade-off between the extent of soil exploration and the efficiency of soil occupation.

To test our first hypothesis, we developed a model of a plant that take up phosphorus and increases its availability through the exudation of citrate (Hinsinger, 2001; Raynaud et al., 2008). The case of citrate is well documented (Hinsinger, 2001) and is a case where the effect of exudate on nutrient cycling do not involve soil microorganism [lien chapitre1]. We used a modelling approach derived from the Barber-Cushman models (Raynaud and Leadley, 2004; Raynaud et al., 2008; Barber and Cushman, 1981), which simulates in a volume of soil of a few cm^3 the uptake of phosphorus by roots, the exudation of citrate, the diffusion of solutes (exudates and nutrients), the solubilization of phosphorus and losses due to leaching and uptake by microorganisms. Interactions between roots were characterized by comparing nutrient uptake efficiencies for a wide range of root densities. The role of rhizosphere sizes on inter-root interactions was also tested by using different levels of soil water content (that affected solutes mobility) and of root activity.

In order to test the hypothesis of a trade-off between soil exploration and occupation, we used a simple method to upscale processes from the rhizosphere scale to the belowground ZOI (Darrah et al., 2006). Soil exploration was quantified by the horizontal extent of the belowground ZOI (we did not consider variations in vertical exploration). Within the belowground ZOI, root length density was more or less heterogeneous, as a function of architectural development. Here we consider the case of a root system where root density decreases from the plant stem (Casper et al., 2003). Often nutrient foraging studies consider plants that adjust roots development to pre-existing heterogeneous pattern of nutrient distribution (Hodge, 2006). Here, here to focus on one type of processes, we considered an initially homogeneous distribution of nutrients in soil that becomes heterogeneous as a consequence of root exudation. We did not consider inter-plant competition so that soil occupation was only quantified as the ability of a plant to maximise phosphorus availability and minimise its losses by leaching and uptake by microorganisms.

4.3. Material & Methods

4.3.1. Model Description

We used the PARIS model framework (Raynaud et al., 2008; Raynaud and Leadley, 2005, 2004), inherited from the Barber-Cushman approach (Barber and Cushman, 1981; Tinker and Nye, 2000). The model simulates rhizosphere processes, including diffusion, absorption, exu-

Table 4.1.: Summary of model parameters and the values used for simulations

	name	meaning/definition	units	range/value
soil	h	root radius	cm	0.01
	z	thickness of soil	cm	1
	θ	volumetric soil water content	$cm^3.cm^{-3}$	0.06–0.15
	θ_{th}	soil water content threshold	$cm^3.cm^{-3}$	0.05
	ρ	soil density	$g.cm^{-3}$	1.16
exudate	D_{cit}	diffusion coefficient in pure water	$cm^2.s^{-1}$	$6.2\ 10^{-6}$
	$K_{d,\,cit}$	distribution coefficient	$cm^3.g^{-1}$	4.4
	μ_{cit}	decay rate	s^{-1}	10^{-5}
	K_C	half saturation constant of the bioavailability factor	$mmol.cm^{-3}$	10^{-5}
nutrient	D_P	diffusion coefficient in pure water	$cm^2.s^{-1}$	$8.2\ 10^{-6}$
	$K_{d,\,P}$	distribution coefficient	$cm^3.g^{-1}$	82.6
	μ_P	loss rate	s^{-1}	$0–10^{-2}$
	S_{min}	minimum soil supply	$mmol.cm^{-3}.s^{-1}$	10^{-12}
	S_{max}	maximum soil supply in presence of a chemical factor	$mmol.cm^{-3}.s^{-1}$	$5\ 10^{-10}$
root	I_{max}	maximum root uptake rate	$mmol.cm^{-2}.s^{-1}$	$2\ 10^{-8}$
	K_M	half saturation constant for root uptake	$mmol.cm^{-3}$	10^{-4}
	e_{cit}	exudation rate	$mmol.cm^{-2}.s^{-1}$	10^{-10}–10^{-8}
	n_{root}	root length density	$cm.cm^{-3}$	0–30
plant	n_{tot}	total root length	cm	5000–15000
	r_{max}	maximum root lateral spread	cm	20–40
	β	decreasing factor for root density	cm^{-1}	0–0.1

Table 4.2.: Summary of model variables. These variables can be used at different scales: the voxel (nutrient and exudate variables), the simulated soil volume and the whole volume explored by plants (all variables).

	name	meaning	units
nutrient	C_P	concentration in soil solution	$mmol.cm^{-3}$
	S_P	nutrient supply	$mmol.s^{-1}$
	L_P	nutrient losses	$mmol.s^{-1}$
	A_P	nutrient absorption	$mmol.s^{-1}$
	U_P	nutrient uptake efficiency	$mmol.cm^{-2}.s^{-1}$
	A_P/S_P	nutrient cycling efficiency	*none*
exudate	C_{cit}	concentration in soil solution	$mmol.cm^{-3}$
	E_{cit}	total exudation	$mmol.s^{-1}$
	L_{cit}	total decay of exudates	$mmol.s^{-1}$
soil occupation ratios	$rhiz_P$	proportion of soil within the P depletion rhizosphere	%
	$rhiz_S$	proportion of soil within the increased P supply rhizosphere	%

dation, and chemical reaction within the soil solution. Model parameters and variables are summarized in tables 4.1 and 4.2.

Roots are assumed to grow vertically down into the soil, and no root branching occurs within the simulated soil volume. The model thus describes a small 1 cm thick (parameter z) layer of soil with a surface of 2x2 cm. It is organized on a rectangular grid of voxel that can be either soil or root, whose widths (parameter h) are equal to the diameter of roots. Soil heterogeneity is considered horizontally only. To avoid edge effects, we consider the surface modelled as a torus.

The diffusion of solutes (phosphorus and citrate) only occurs within the liquid phase of the soil and is thus a function of soil water contentθ. For a given solute i, the effective diffusion coefficient of solutes within the soil $D_{e,\,i}$ is calculated from soil density ρ, the solute diffusion coefficient in pure water D_i and distribution coefficient $K_{d,\,i}$ (table 4.1) (Van Rees et al., 1990; Raynaud et al., 2008):

$$bD_{e,\,i} = D_i \theta \, f_l \tag{4.1}$$

with soil buffer capacity (that quantifies interactions between soil solution and the solid phase).

$$b = \theta + \rho \, K_{d,\,i} \tag{4.2}$$

and soil tortuosity

$$f_l = 1.1(\theta - \theta_{th}) \tag{4.3}$$

Each solute has a loss rate μ_i, which expresses the decay of citrate and both consumption by other organisms or leaching for phosphorus.

Roots absorb nutrients from adjacent soil voxels following a Michaëlis-Menten equation (parameters I_{max} and K_M), where C_P is the concentration in nutrients in the soil voxel:

$$U_P = I_{max} \frac{C_P}{C_P + K_M} \tag{4.4}$$

Exudation rate per unit of root surface is constant and expressed by parameter E_{cit}. In the absence of citrate, nutrient supply within the soil S is expressed by the constant S_{min}. In the presence of the citrate, phosphorus supply is increased according to (Raynaud et al., 2008):

$$S_P = S_{min} + (S_{max} - S_{min}) \frac{C_{cit}}{C_{cit} + K_C} \tag{4.5}$$

4.3.2. Numerical analysis

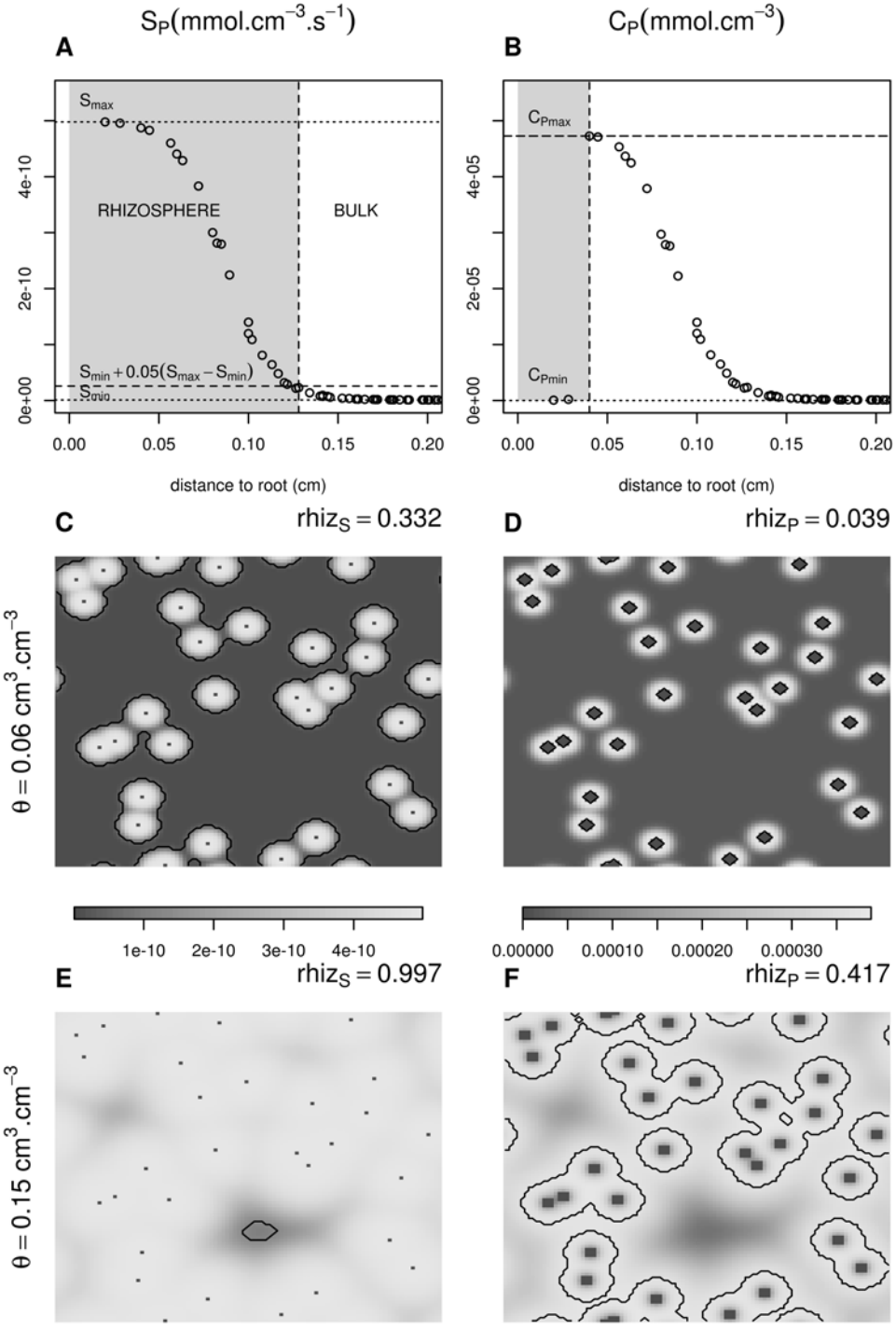
The model was coded in JAVA, within the 3Worlds modelling platform (Gignoux et al., 2005). 3Worlds is a generic simulator able to represent any kind of ecosystems, based on a re-analysis of the ecosystem concept (Gignoux et al., 2011). Its architecture enables the modeller to only focus on the ecology, while providing a full graphical user interface and an individual-based framework and API (Application Programming Interface) where biological and physical processes can be coupled together. To implement Paris within 3Worlds, individual roots were randomly distributed within a 2-dimensional grid of cells representing a layer of soil. Solutes diffusion (O'Reilly and Beck, 2006) and root-soil interactions (absorption and exudation) were programmed as reusable sub-routines plugged into the 3Worlds core application. The time step for integration was 10 s. Phosphorus and citrate parameters were taken from (Raynaud et al., 2008) and different values of μ_P were tested (table 4.1). We modelled rhizosphere processes for a gradient of root densities ranging from 1 to 40 roots per cm^{-3}, with roots placed randomly within the 2x2 cm modelled surface. To test the effect of root distribution on the results, 3 different maps where tested for each n_{root} value. As soil water content affects the diffusion of solutes (equations 4.1 to 4.3), hence the sizes of the rhizospheres, our simulations were done for two values of this parameter (table 4.1). We also tested different values for the exudation rate, e_{cit}, that affects the size of the exudation rhizosphere and that quantifies plant investment in the control of phosphorus availability.

The model was solved numerically until an equilibrium between all the fluxes of nutrient and exudate was reached. For each simulation, the influx, stocks and outflow of solutes were calculated for both phosphorus and citrate (Table 4.2). In particular, we quantified plant nutrient uptake by three distinct variables:

1. total plant uptake A_P.
2. nutrient uptake efficiency U_P (nutrient uptake per unit of root surface).
3. nutrient cycling efficiency, defined as the proportion of nutrient input to the system that is absorbed by roots A_P/S_P. Note that at equilibrium, this ratio is also related to nutrient losses:

$$\frac{A_P}{S_P} = 1 - \frac{S_P - A_P}{S_P} = 1 - \frac{L_P}{S_P} \tag{4.6}$$

Figure 4.1.: Illustration of the method used to calculate the rhizosphere size for the impact of root on phosphorus supply S_P (A, C & E) and depletion (B, D & F). Panels A and B show the gradient of S_P and phosphorus concentration C_P from the surface of a root to the surrounding bulk soil. In A, the border of the rhizosphere is set at 0.95% of the difference with bulk soil level whereas in B, it is set at the maximum of nutrient concentration. Panels C to F represents soil maps for two simulations differing only in soil water content θ, with their respective estimations of the proportion of the soil area within the rhizosphere $rhiz_P$ and $rhiz_S$. Roots are figured by an empty cell and the dark lines figures the calculated limit for their rhizosphere.



Our simulations also yielded maps of phosphorus and citrate concentrations C_P and C_{cit}, from which the border of the rhizosphere of individual roots could be calculated (figure 4.1). To do so, we had to consider that (i) the size of the rhizosphere depends on the process considered and (ii) the border between the volume of soil influenced by root and bulk soil has to be drawn arbitrary (Hinsinger et al., 2009). To quantify the impact of roots on phosphorus supply within the soil solution, we measured the rhizosphere directly from the pattern of nutrient supply – deduced from the C_{cit} map and equation 4.5 – rather than from citrate distribution directly. In this case, we fixed the border of the rhizosphere as the isocline of 5% soil modification by roots compared to bulk soil values (Figure 4.1, panel A). We also calculated the nutrient depletion rhizosphere and fixed its border to the local maximum of nutrient concentration (panel B). Variables $rhiz_S$ and $rhiz_P$ quantify the proportion of soil surface within the rhizosphere, as estimators of soil occupation for phosphorus supply and phosphorus uptake, respectively. We also calculated the $rhiz_P/rhiz_S$ ratio, which represents the proportion of the phosphorus supply rhizosphere that is depleted by roots over the area of soil modelled. Panels C to F of figure 4.1 show an example of soil occupation calculation for two contrasted values of soil water content θ.

4.3.3. Upscaling rhizospheres to the below-ground zone of influence

Figure 4.2.: Model of root density distribution at the scale of the whole system. Panel A explains the upscaling method: we considered an exponentially decreasing densities from the plant stem organized in concentric rings 5 cm (parameter dr) wide. Table 4.3 shows the increasing surfaces of these rings. Panel B shows the root profiles modelled in our study, where we used different values of decreasing coefficient β, maximum root lateral spread r_{max} and total root length n_{tot}.

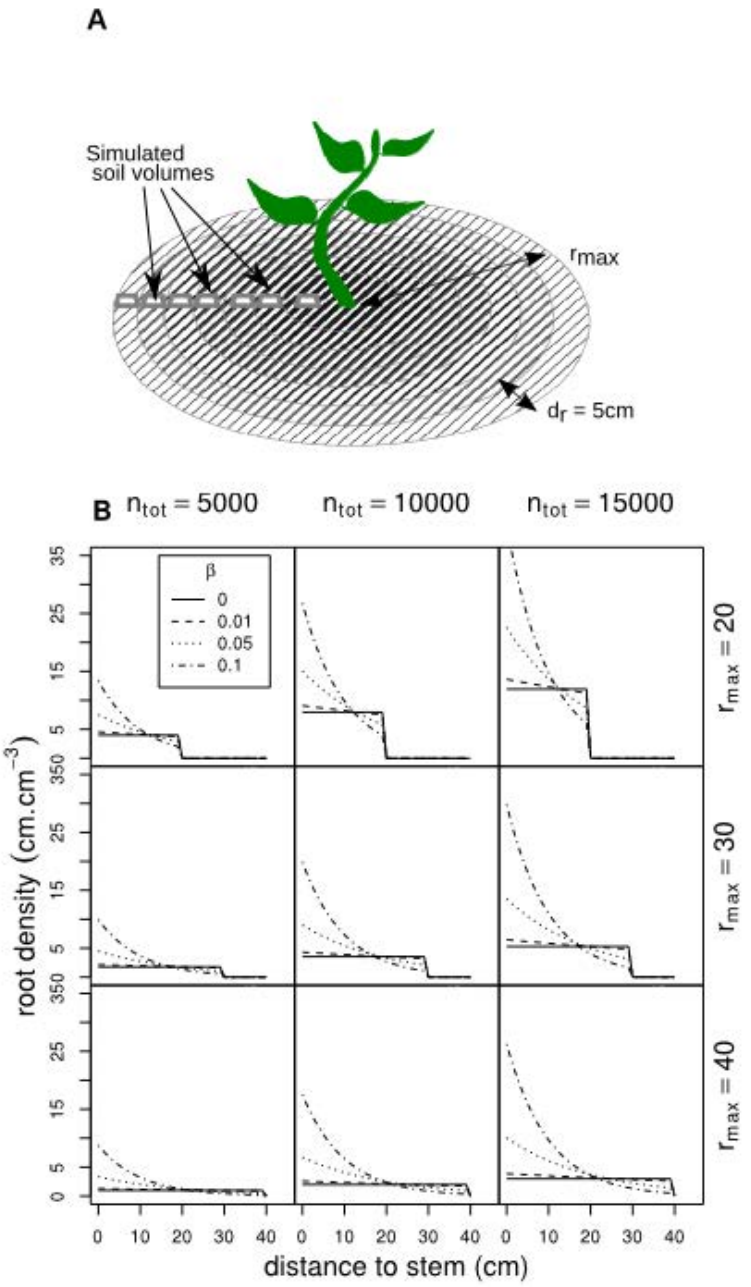


Table 4.3.: Surfaces of concentric rings from the plant stem, that were used to weight the results of simulations in the upscaling process. See figure 4.2

ring	surface (cm^2)
0-5	78.5
5-10	235.6
10-15	392.7
15-20	549.8
20-25	706.9
25-30	863.9
30-35	1021
35-40	1178.1

We considered a horizontal gradient of root distribution, with root distribution organized in concentric rings of decreasing root density from the plant stem outwards (Figure 4.2 and table 4.3). Field data quantifying root zones of influence (Casper et al., 2003; Hartle et al., 2006) suggest exponentially decreasing root densities. We thus used the following relation for root length densities as a function of the distance to plant stem:

$$d(r) = d_0 e^{-\beta\, r},\ r \in [0, r_{max}] \tag{4.7}$$

We considered different values for the decreasing factor β, including the case for which roots are uniformly distributed ($\beta = 0$). The maximum root lateral spread r_{max} circumscribes the belowground zone of influence and quantifies the extent of soil exploration. Density at the plant centre d_0 was calculated so that the total root length within the volume of soil explored reached chosen values (n_{tot}, table 4.1). Assuming that rhizosphere processes at different distances are independent, we extrapolated model outcome at the plant scale from the simulations at the rhizosphere scale. The contribution of each ring to total uptake was calculated by weighting modelled soil volume outcome by the surface of the corresponding ring (figure 4.2, panel A). Root lateral spread values were chosen following (Schenk and Jackson, 2002), with values within the range of perennial grasses under tropical climates. These plants have a relatively narrow exploration pattern (Schenk and Jackson, 2002) and have a more or less localised root distribution, which may induce different ability to control phosphorus availability and uptake (chapter 3.6). We calibrated the range of root length densities from data of different species of the *Poaceae* family (*Hyparrhenia filipendula* and *Heteropogon contortus*) in the savannah ecosystem of Hwange in Zimbabwe (chapter 3.6).

4.4. Results

4.4.1. Root density effects on nutrient uptake at the centimetre scale

In our model, the total phosphorus uptake A_P always increases with increasing root length density n_{root} and exudation rate e_{cit} and decreasing phosphorus losses μ_P (figure 8.1 in the appendix). This result is not surprising, as the input of available phosphorus within the soil solution depends mostly on root exudation. A_P values are higher when $\theta = 0.15$ than when $\theta = 0.06$, which can be explained by the fact that root exude citrate that diffuses within a larger volume, which yields higher inputs of phosphorus S_P (figure 8.2 in the appendix).

When there is no phosphorus loss ($\mu_P = 0$), so that phosphorus supply equals its uptake, phosphorus uptake efficiency U_P decreases with increasing root length densities n_{root} (figure 4.3, panel A, top). Even if the plant always get more phosphorus by increasing root length density n_{root}, the more roots, the less nutrients each one gets, which decreases the benefits of the construction of new roots compared to their costs. In the following, we define root competition as a negative relationship between U_P and n_{root}.

When $\mu_P > 0$ (figure 4.3, panel A, middle and bottom), phosphorus uptake efficiency either decreases, increases or remain stable with increasing root length density. We define positive relationships between n_{root} and U_P as cases of synergy between roots, or root facilitation: the more roots, the more efficient they are in taking up nutrients. This case is observed for $\theta = 0.15$ and is favoured by low exudation rate e_{cit}, and high phosphorus losses rate μ_P. Note however the same kind effects of effect of θ and μ_P is observed for U_P than for A_P (figures 4.3, and 8.1 in the appendix. As a consequence, the positive relationship occurs for much lower values of uptake rate and nutrient uptake efficiency.

Interestingly, the variability of U_P increases once a threshold value of n_{root} is reached, whose value depends on θ and μ_P. Above this threshold, the spatial distribution of roots has a stronger influence on the type of interactions than their density.

The nutrient cycling efficiency of the system A_P/S_P always equals 1 when $\mu_P = 0$ as the only way of a phosphorus molecule to get out of the soil solution is by getting absorbed by a root. When $\mu_P > 0$, A_P/S_P always increases with root density (figure 4.3, panel B). Unlike A_P and U_P, A_P/S_P increases with decreasing soil water content θ and phosphorus losses μ_P.

Figure 4.3.: Phosphorus uptake efficiency U_P (panel A) and cycling efficiency A_P/S_P (panel B) as a function of root density n_{root} for different parameter values tested in the study: exudation rate e_{cit}, mineral nutrient losses μ_P and soil water content θ.

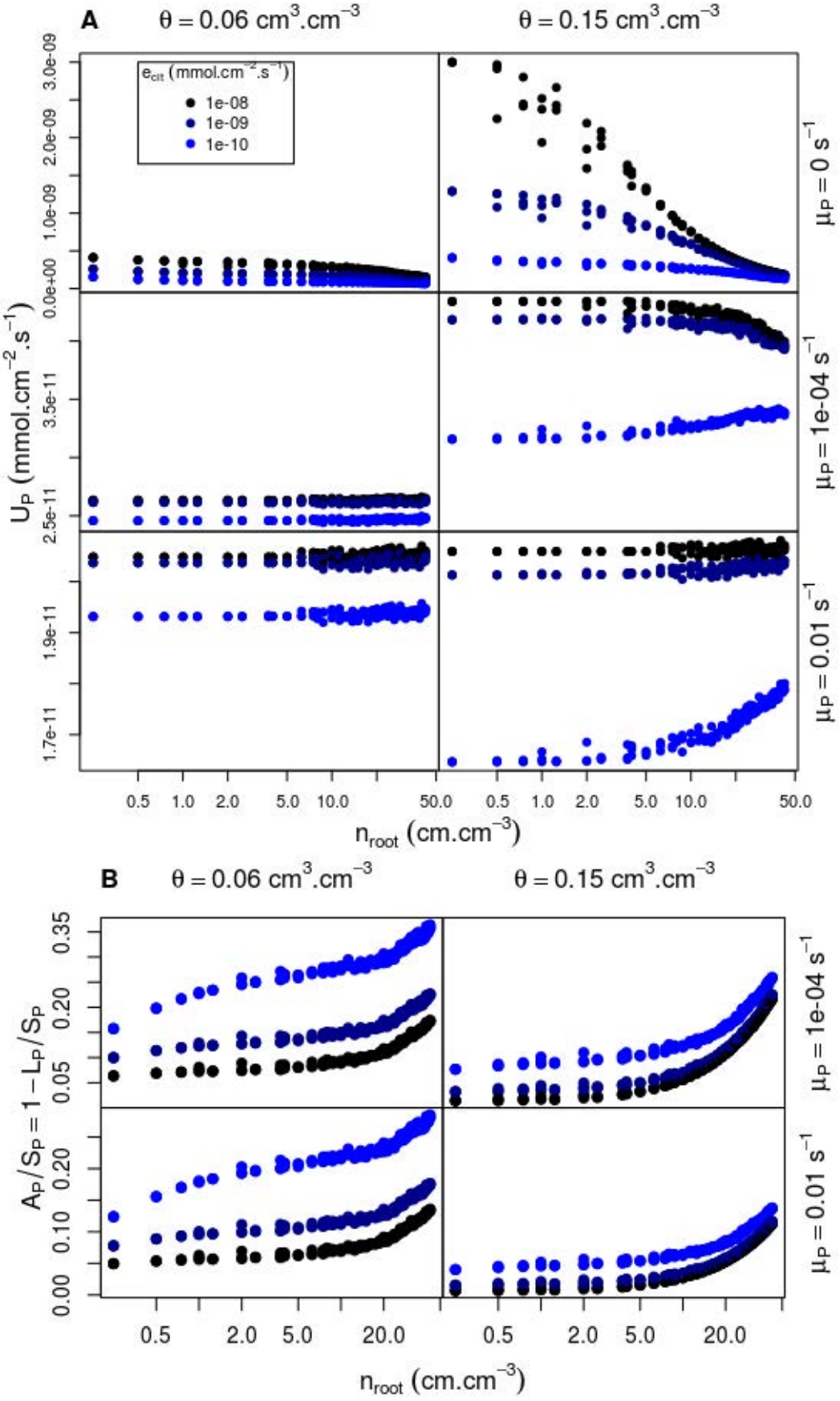
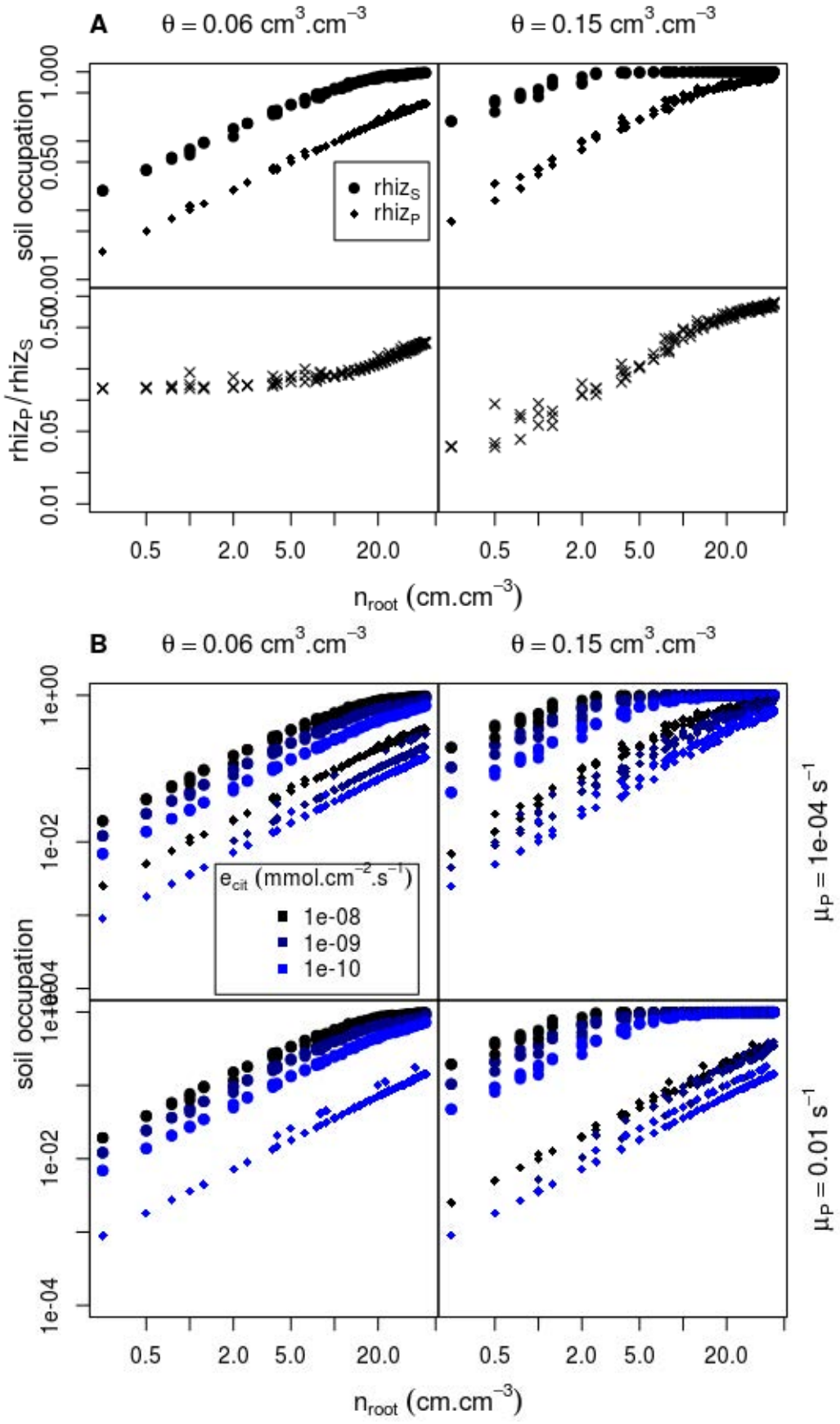


Figure 4.4.: Log/log plots of different soil occupation ratios as a function of root density n_{root}. Panel A focuses on the case where exudation rate $e_{cit} = 1e-8$ mmol.cm^{-2}.s^{-1} and phosphorus losses rate $\mu_P = 1e-4$ s^{-1} and shows the relations between $rhiz_S$, $rhiz_P$ and the ratio $rhiz_P/rhiz_S$ for the two values of soil water content θ tested. Panel B shows the values of $rhiz_S$ and $rhiz_P$ for different values of e_{cit} and the two strictly positive values of μ_P tested in this study.



4.4.2. Rhizosphere sizes as predictors of root interactions

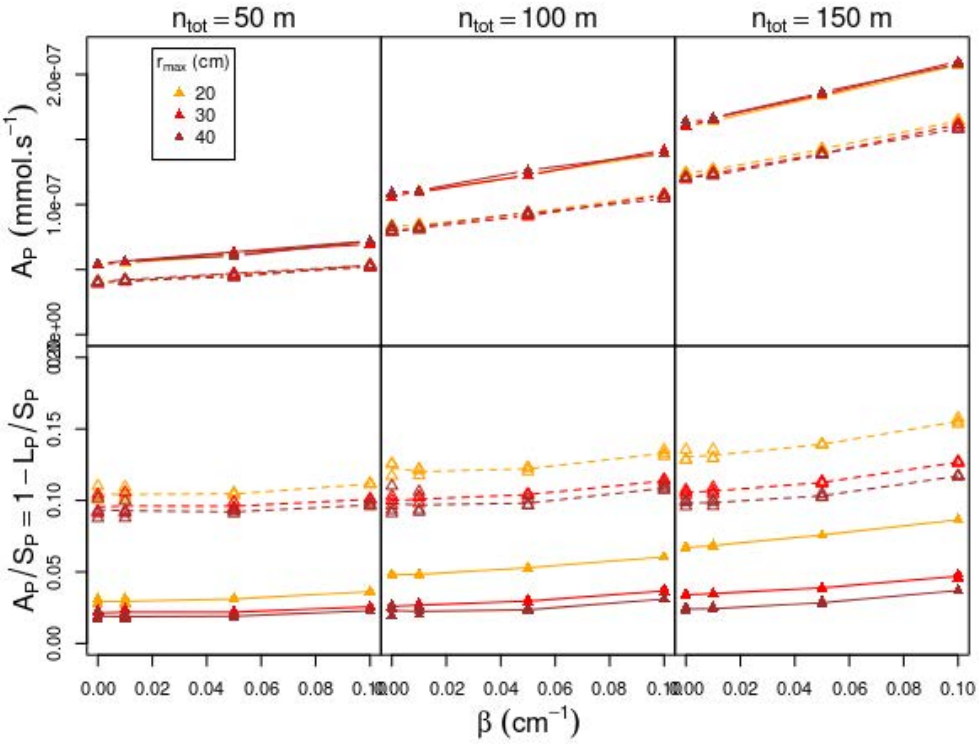
Figure 4.4, panel A, illustrates changes in the rhizosphere extension as a function of soil water content θ and root length density n_{root}. By construction, the depletion rhizosphere $rhiz_P$ is smaller than the nutrient supply rhizosphere $rhiz_S$ (figure 4.1). For low root length densities n_{root}, $rhiz_S$ and $rhiz_P$ increase linearly with the same rate. In this range of root densities, the ratio $rhiz_P/rhiz_S$ is relatively constant and corresponds to the ratio of phosphorus depletion rhizosphere by nutrient supply rhizosphere of a single root. It starts to increase when root length densities are sufficiently high so that phosphorus supply rhizospheres overlap, but not phosphorus depletion rhizospheres. This first threshold is a function of soil water content θ and matches with the threshold described in paragraph 4.4.1 and figure 4.3, panel A. $rhiz_S$ reaches a maximum value of 1 when all the soil modelled is under the influence of exudated citrate. However, the effect of citrate has not reached saturation at this threshold and phosphorus supply S_P still increases for higher values of n_{root} (figure 8.2). In the case where $\theta = 0.15$ cm^3.cm^{-3}, we reached root densities when root deplete phosphorus over the whole area of soil, leading to a saturation of both $rhiz_P$ and $rhiz_P/rhiz_S$.

We made the hypothesis that the patterns of $rhiz_P$, $rhiz_S$ and $rhiz_P/rhiz_S$ could be used to explain or predict the type of interactions between roots (competition vs. facilitation). Cases of facilitation obtained in this study occurred for high values of n_{root} (figure 4.3) and high soil water content, that favours the diffusion of citrate ($\theta = 0.15$, see equations 4.1-4.3). In these cases, all the soil is under the influence of roots (high $rhiz_S$). An other condition is that exudation is sufficiently low ($e_{cit} = 1e^{-8}$) so that phosphorus supply S_P is not saturated (figure 8.2 in the appendix). Finally, phosphorus losses tend to increase the slopes of the relation between U_P and n_{root}, which can be linked to lower values of $rhiz_P$: individual roots are less bound to overlap each other's phosphorus depletion rhizosphere. Contrary to our expectations, the patterns of $rhiz_P/rhiz_S$ does not seem to provide useful information to discriminate cases of competition from cases of facilitation (figure 8.3 in the appendix).

4.4.3. Root foraging at the scale of the below-ground zone of influence

We compare here two close parameter sets, differing only by two exudation rates, resulting in contrasted inter-root interactions: competition between roots for nutrient uptake or facilitation between roots by increasing nutrient supply (figure 4.3). At the whole plant scale, total phosphorus uptake, A_P, increases with the size of the root system, n_{tot}, and the decreasing factor β

Figure 4.5.: Overall phosphorus uptake A_P and cycling efficiency A_P/S_P as a function of plant exploration parameters: the total length of the root system n_{tot} (with values of 50, 100 and 150 m from left to right), the decreasing factor of root density β and maximum root lateral spread r_{max}. We focus here on the case where the phosphorus losses rate $\mu_P = 1e^{-4}$ and soil water content $\theta = 0.15$, for two exudation rates e_{cit} for which inter-root interactions are either competitive ($e_{cit} = 1e^{-8}$) or facilitative ($e_{cit} = 1e^{-10}$– see figure 4.4.1, panel A). The case of facilitation is figured by empty triangles and dashed lines.



(figure 4.5, up). A_P was more influences by n_{tot} than β, while no strong effect of maximum root lateral spread r_{max} was found. Nutrient uptake efficiency displayed the same patterns (figure 4.5, down), except for the effect of the root system size (figure 8.4 in the appendix). Nutrient cycling efficiency A_P/S_P was much more influenced by r_{max} than by n_{tot} and β. In all cases considered, the root systems that minimized the most nutrient losses where the less spread (lowest r_{max}).

4.5. Discussion

4.5.1. Inter-root competition and facilitation

The first important result of our study is the confirmation of our first hypothesis: under determined conditions, synergies can emerge between individual roots of a plant, *via* the interplay between uptake and exudation. In our simulations results, total nutrient uptake and nutrient cycling efficiency were always increasing with root densities, but nutrient uptake efficiency either increased of decreased, depending on the parameter values. We interpreted these patterns in terms of inter-root facilitation or competition. The concept of competition between parts of a plant has two distinct meanings in plant science. It is involved in the reproduction and evolutionary strategies of plants, were allocation of resources within the plant matters (e.g. vegetative vs. reproductive parts) (Sadras and Denison, 2009). When applied to the study of root architecture, it expresses the fact that the proximity of depletion zones of different parts of the root system lowers their respective uptake efficiencies (Ge et al., 2000). The application of the concept of facilitation at the rhizosphere's scale is rare (Hinsinger, 2012). To our knowledge, this is the first time this concept is applied to the roots of a plant. We show that the ability of a plant to increase nutrient availability does not prevent root competition, but rather creates a continuum between cases of inter-root competition and inter-root facilitation.

Soil occupation ratios ($rhiz_P$ and $rhiz_S$) were useful tools to explain relationships between root densities and phosphorus uptake efficiency. Surprisingly, the ratio between these two areas was not informative. Our results suggest that inter-root facilitation is favoured when exudation rhizospheres overlap without saturating phosphorus supply, and where roots are distant enough so that phosphorus depletion zones do not overlap. The outcome of inter-root interaction is thus a subtle function of the rhizosphere sizes of individual roots and their overlap.

Rhizosphere size is a function of the rates of citrate exudation and phosphorus uptake – although not tested here – and of soil water content(Raynaud, 2010). The highest value of soil water content favoured the overlap of exudation rhizospheres, which lead to inter-root facilita-

tion. We can make the hypothesis that a excessive soil water content would favour inter-root competition, by increasing the overlap of depletion rhizospheres (Ge et al., 2000). Low values of citrate exudation favoured facilitation, as it avoided saturation of phosphorus supply. The function that relates phosphorus supply to citrate concentration is thus a key element of the model. Rhizospheres overlap is a function of root length densities, root distribution, and soil water content. In cases where soil water content was the lowest and thus rhizosphere sizes where very small, the nutrient uptake efficiency of roots was more influenced by the distribution of roots than by root length density.

A necessary condition for the existence of facilitation is a non null rate of phosphorus losses. Otherwise, any increase of phosphorus supply benefits directly to the plant. When this rates increases, facilitation seems more favoured, since denser roots systems reduce the mean distance between where an available phosphorus molecule is produced and where it is taken up,reducing its probability to be lost for the plant.

Our study focused on the case of phosphorus uptake and the control of its availability by the exudation of citrate. The concept of facilitation within rhizosphere processes could also apply to other nutrients and effects of root on soil processes (e.g.(Hinsinger, 2001)). Our results suggest that root facilitation should occur mainly for low diffusive nutrients, whose nutrient depletion zones are less bound to overlap. Increased phosphorus availability due to citrate exudation is a case where plants act directly on chemical reactions within the soil. Mineralisation or nitrification are also a process that plants control through exudation and that increases nutrient availability (Fontaine et al., 2007; Subbarao et al., 2006). In this case however, plants rely on the activity of soil microorganisms. This induces at least two differences with the system studied in this paper. First, the entity (or group of entity) that increases nutrient availability directly compete with the plant for it, depending for example on the C:N ratio of soil organic matter (Bardgett, 2005). Second, we can expect a higher delay between exudation of carbohydrates and the increase in nutrient availability. In such case, a proximity between roots differing in their developmental stage would be profitable for the plant (Clarholm, 1985; Raynaud et al., 2006).

4.5.2. Inferring optimal root strategies

Our modelling approach yielded patterns of phosphorus uptake rate, uptake efficiency and cycling efficiency as a function of root length density. Each of these patterns can be mobilized in the estimation of optimal root strategies in the exploitation of a given volume of soil, depending on whether one considers a plant foraging nutrients alone, or in the presence of other plant

competitors. In the first case, an optimal root strategy can be defined as the adjustment of the architecture and the activity of the root system that maximizes the uptake of the targeted nutrient, with the lowest possible costs due to root construction and functioning (Lynch and Ho, 2005). Optimal root proliferation and activity can be deduced from the relation between nutrient uptake efficiency and the length of root invested, but also from the respective costs of nutrient uptake and exudation. Even if systems with low exudation rates showed lower uptake efficiencies than high exudation systems, they might be favoured if the cost of exudation is high compared to root construction. Nutrient cycling efficiency (the proportion of nutrient supplied to the system that is absorbed by roots) is a possible quantification of the efficiency of root exudation. It was always higher for low than for high exudation root systems and increased with root densities. This suggest that having high roots length densities and low exudation rates can be an efficient strategy for a plant, that minimizes nutrient losses from the system. This is a possible explanation of cluster roots (Lambers et al., 2006), where plants develop a high surface of interaction with the soil in a very small volume.

In the case of competition between plants sharing a given volume of soil, foraging strategies are assessed by the ability of a plant to outcompete its neighbours. In this case, a plants tends to maximise their total nutrient uptake, which often leads it to invest more carbon in roots than optimal (Robinson et al., 1999; Gersani et al., 2001). The combined effect of nutrient uptake and exudation and their respective rhizosphere sizes adds complexity in the prediction of the outcome of competition (Raynaud et al., 2008).

In this study, the representation of the root system was simplified and we focused on the horizontal distribution of roots. Coupling architectural models to rhizosphere quantification as in Pagès (2011) can help to take the development of the root system with time and the architectural constraints of root growth into account. One aspect of the rhizosphere that has not been developed in this study is its temporal dynamics: often, exudation and absorption do not occur in the same parts of each individual root Doussan et al. (2003); Hinsinger et al. (2009).

The turnover rate of roots is also an important component of root strategies (Frank and Groffman, 2009) . Although our approach is not dynamic – due to methodological constraints we only considered systems in a dynamic equilibrium –, our results underline that nutrient uptake efficiencies, as a function of rhizosphere sizes, is strongly affected by soil water content, a parameter that varies greatly over time (Loague, 1992). The turnover of roots may thus help plant to adjust their strategies to such temporal variations. Root turnover can also be explained by the life-span of the resource pool: structures that efficiently take up a finite resource such as

cluster roots are short-lived (Lambers et al., 2006).

4.5.3. The exploration/occupation trade-off

Our second hypothesis was that the combination of nutrient uptake and the control of nutrient availability by exudation could lead to a trade-off between the extent of soil exploration – that determines plant access to the pools of nutrients – and the intensity of soil occupation – the ability of plants to properly exploit these pools. This trade-off can be interpreted as a generalization of the guerilla vs.phalanx metaphor (Harper, 1980; Clegg, 1978) to the general context of nutrient foraging. This trade-off can be understood differently whether one consider the ability of plant to increase phosphorus availability, to maximise the efficiency of phosphorus uptake or to minimise phosphorus losses in the process. Over the range of root distributions tested in our study, nutrient cycling efficiency was negatively correlated to root maximum lateral spread. This was not the case for total nutrient uptake and nutrient uptake efficiencies that were more affected by the decreasing factor of root density (β). In these cases, the most efficient root systems were the most heterogeneous ones. Our hypothesis of a trade-off between exploration and occupation applied more to the ability to have a closed phosphorus cycle, with reduced losses, than a system that maximise phosphorus uptake. Interestingly, this general pattern did not depend on whether we had facilitation or competition between roots. The advantage to the most heterogeneous system arises either because they minimise negative interactions among roots, or because they allow locally the maximisation of positive interactions between roots.

Our modelling approach can be applied to any process involving the diffusion of exudates in the soil, that yield a benefits for roots. It can be applied to cases such as allelopathy, where plant occupy soil by interference with neighbour plants (Schenk, 2006). Another example is the biological inhibition of nitrification (Subbarao et al., 2006), which is associated with a preference for ammonium. As the efficiency of BNI increases with root concentration (Lata et al., 2000) and that ammonium is generally less mobile than nitrate, one should expect that plant inhibiting actively nitrification should have more concentrated root systems.

4.5.4. Conclusion

Our study shows that interactions between individual roots is not necessarily competitive but can also become facilitative in some contexts. It thus give a wider range of mechanisms that must be taken into account to interpret root foraging strategies and possibly the outcome of

plant-plant interactions. Reaching this result required taking into account both root exudation and absorption, and their respective spatial scales. In some cases, there is a trade-off between soil exploration and occupation, which can be related to two contrasted strategy in terms of nutrient cycling: the maximization of nutrient absorption and an optimal consumption of soil resources.

4.6. Acknowledgement

We thank Shayne Flint and Ian Davies for their help in designing the model on 3Worlds. This work was funded by the ANR 3Worlds.

Perspectives

Cette étude a permis de mettre en évidence des relations entre densité racinaire et efficacité d'absorption racinaire. Les résultats obtenus suggèrent également un effet important de la distribution des racines. La distance moyenne entre racines conditionne en effet le chevauchement entre rhizosphères, et dépend à la fois de la densité des racine, et de la distribution, uniforme ou agrégée. Cet aspect peut être exploré par l'usage d'un plus grand nombre de cartes racinaires.

Dans cette étude, les mêmes portions de racines exsudaient et absorbaient les nutriments. Cette hypothèse peut être relâchée dans le même cadre de modélisation, en considérant différents types racinaires : racines exsudantes et/ou absorbantes. La mortalité racinaire peut être également prise en compte, en considérant les racines mortes comme des sources de nutriments, d'une durée de vie donnée. Dans le cadre de 3World, ce changement peut être fait par la création d'un module de démographie racinaire. Cela impliquera cependant d'analyser la dynamique des systèmes et non leur état d'équilibre comme dans le dernier chapitre.

Enfin, le niveau basal d'apport du phosphore est extrêmement faible dans le cadre de cette étude, ce qui fait que l'exsudation est absolument nécessaire pour la nutrition des plantes. Il peut être intéressant d'élever la disponibilité des nutriments en l'absence d'exsudation, pour comparer l'efficacité de différentes stratégies d'exploration racinaire, selon que les plantes absorbent uniquement les nutriments déjà disponibles ou investissent dans l'exsudation de manière à augmenter sa disponibilité.

Discussion et Perspectives

5. Discussion Générale

Le travail de cette thèse a consisté à mettre en relation la capacité des plantes à contrôler les cycles de nutriments minéraux et leur mode d'exploration racinaire. J'ai développé à cette fin une approche spatialisée, en considérant les interactions entre racines et sol à l'échelle fine de la rhizosphère (chapitre 4) ou à celle de la zone d'influence souterraine d'une plante (chapitres 3 & 4) ou de populations (chapitre 2). J'ai suivi **trois approches méthodologiques distinctes et complémentaires** : la modélisation mathématique (chapitre 2) ou numérique (chapitre 4) et le travail de terrain (chapitre 3). Les perspectives de travail immédiates relatives à ces approches ont déjà été développées dans les perspectives des chapitres correspondants. La première partie de cette discussion générale vise à montrer dans quelle mesure les différentes approches développées permettent de répondre aux deux questions générales de cette thèse (Cf chapitre 1) :

1. Dans quelle mesure la capacité des plantes à influencer le recyclage des nutriments est impliquée dans les stratégies d'exploration racinaire ?
2. Quelles sont les conséquences, en retour, des patrons d'exploration des racines sur le recyclage des nutriments dans les systèmes plante-sol ?

Je me suis restreint dans cette thèse à la question des **interactions entre exploration racinaire et cycles des nutriments**. La seconde partie de cette discussion explore la question plus générale des **liens entre rétroactions plante-sol et stratégies d'acquisition des nutriments** chez les plantes. Cela me permet d'estimer la portée plus générale des concepts, hypothèses et approches de cette thèse, en particulier pour des communautés végétales complexes et dans une vue d'application de ces théories en termes de gestion des écosystèmes. En guise de conclusion, je résumerai les principaux apports de cette thèse à la compréhension du fonctionnement des systèmes plante-sol.

5.1. Stratégies d'exploration racinaire et cycles des nutriments

5.1.1. Compétition et facilitation racinaire

Un trait commun aux différents chapitres de cette thèse est de tenter d'articuler les différents mécanismes et échelles d'interaction plante-sol, listés au chapitre 1 (*Cf.* également figure 1.1 et tableau 1.1). Le cas le plus simple est celui de segments de racines, qui n'affectent pas le même volume de sol selon que l'on considère l'abaissement de la concentration de nutriments absorbés ou l'exsudation d'éléments favorisant la disponibilité de ceux-ci. **Cela m'a amené au chapitre 1 à formuler l'hypothèse de synergies entre racines d'une même plante**, que j'ai testée au chapitre 4 au travers du cas d'une plante libérant du citrate et absorbant du phosphore.

L'usage de la modélisation informatique (chapitre 4) nous a bien permis d'établir des relations entre densités racinaires et efficacité de la nutrition des plantes et du recyclage des nutriments. J'ai pu ainsi mettre en évidence des situations de synergies entre racines, selon le contenu en eau du sol, le taux d'exsudation et les pertes en nutriments. Ce résultat **suggère l'existence d'un continuum entre des cas de compétition entre les racines d'une même plante** (déjà décrits Ge et al. 2000) et des cas de facilitation entre racines d'une même plante (Hinsinger, 2012). Un autre avantage lié à la méthode utilisée a été de **pouvoir distinctement quantifier les tailles des différentes rhizosphères** (rayon d'augmentation de la disponibilité du phosphore et rayon d'abaissement de la concentration du phosphore), ce qui s'est avéré être un outil pertinent pour expliquer l'émergence de relations positives entre racines d'une même plante.

L'approche de modélisation du chapitre 4 a donc permis de conforter l'hypothèse de synergies racinaires. Ce type de modélisation peut être encore développé, afin d'appliquer cette hypothèse à d'autres nutriments et/ou exsudats. La prise en compte de la démographie racinaire permettrait d'établir sous quelles conditions la proximité des racines permettrait un recyclage efficace des racines mortes par les vivantes (Abbadie et al., 1992), sans que cela ne se fasse au détriment de l'efficacité du prélèvement des nutriments (Ge et al., 2000).

L'hypothèse de synergie entre racines d'une même plante gagnerait également à être testée dans le cadre de modèles représentant explicitement la topologie et la croissance des appareils racinaires (*e.g.* Schnepf et al. 2012; Pagès 2011). Un premier apport de ces modèles est de pouvoir différencier les portions du système racinaire absorbant ou exsudant, qui étaient confondues dans notre approche. Ce type de modélisation permettrait également une confrontation plus directe des données à des observations expérimentale. De nombreuses techniques permettent l'observation de la variation temporelle de rhizosphères *in situ,* maintenant de manière relativement non invasive (Hinsinger et al., 2009). Cependant, un travail important serait à fournir pour pouvoir relier les

observations de rhizosphère à une quantification précise des flux de nutriments dans la zone de sol étudiée. En outre, les techniques d'observation de rhizosphère ne permettent pas encore à ma connaissance de quantifier de manière simultanée plusieurs types de rhizosphère, comme j'ai pu le faire par modélisation.

5.1.2. Intégration des interactions racinaires à l'échelle de la zone d'influence racinaire

Une question récurrente au cours de cette thèse est le passage de l'échelle de la rhizosphère à celle de la zone d'influence racinaire des plantes. L'enjeu de ce changement d'échelle est de pouvoir intégrer l'ensemble des différents mécanismes d'interaction plantes-sol et donc déterminer leurs conséquences sur les stratégies d'exploration racinaire (Darrah et al., 2006). Les chapitres 2 et 4 apportent des éclairages complémentaires à cette question.

Dans le chapitre 4, l'organisation spatiale de l'exploration racinaire est représentée explicitement, à l'échelle d'une plante entière dont la distribution racinaire est limitée par une contrainte architecturale. Dans ce cadre, le changement d'échelle n'entraîne pas la prise en compte de mécanismes d'interaction plantes-sol autres que ceux déjà développés à l'échelle de la rhizosphère. Ce chapitre met donc simplement en évidence les conséquences de l'allocation dans l'espace d'une biomasse racinaire donnée sur le fonctionnement immédiat d'un appareil racinaire et du sol avec lequel il interagit. Mes résultats montrent qu'indépendamment de la question de la distribution initiale des nutriments et du type d'interaction entre racines, **les systèmes où les racines sont disposés de manière hétérogènes tendent à être plus efficaces dans le prélèvement des nutriments et que l'exploration de volumes restreints conduit à réduire les pertes de nutriments** (Fransen et al., 1998).

Dans le chapitre 2, la représentation de l'exploration racinaire est simplifiée en distinguant simplement une zone explorée et non explorée par une population de plantes. Cette démarche permet d'intégrer un plus grand nombre de processus dans une formulation mathématique simple. Le principal avantage de la modélisation mathématique est qu'elle permet une plus grande généralité des prédictions. Ainsi, j'ai pu montrer au chapitre 2 que **l'existence de synergie entre racines n'était pas une condition suffisante pour favoriser un comportement de type "phalange" et qu'il était en plus nécessaire d'être dans des conditions de faible apport en nutriments**.

D'autres approches que celles des chapitres 2 et 4 sont nécessaires pour mieux comprendre le rôle des rétroactions plantes-sol dans les stratégies d'exploration racinaire à l'échelle de la plante

entière. D'un côté, le chapitre 4 ne prend en compte que deux mécanismes d'interaction plante-sol (l'absorption racinaire et l'exsudation). D'autre part, le chapitre 2 est à l'échelle très englobante de la population. Un premier enjeu de telles approches serait de mieux **estimer les coûts du développement et du fonctionnement de l'appareil racinaire** Fitter (1987); Lynch and Ho (2005); Eissenstat and Yanai (1997). En effet, une stratégie ne consiste pas seulement en l'allocation d'une quantité de racines donnée dans un volume donné, mais en l'allocation de matière et d'énergie dans cette construction de racines et dans son fonctionnement (absorption et production d'exsudats). L'exsudation représente un investissement significatif pour les plantes, de l'ordre de 5 à 20% du carbone fixé par photosynthèse (Marschner, 1995). Dans la suite de cette thèse, l'efficacité de stratégies d'exploration et/ou d'occupation du sol pourrait être estimée en comparant les bénéfices fonctionnels d'un système racinaire d'une architecture donnée représenté explicitement, à une estimation appropriée des différents coûts en carbone et nutriments de la construction racinaire, de l'exsudation, *etc.*.

Un deuxième enjeu est une **meilleure prise en compte de l'aspect dynamique du développement de l'appareil racinaire** : la constitution d'un patron d'exploration racinaire n'est pas instantanée, mais est le résultat d'un processus progressif d'adaptation à des conditions du sol, qui peuvent elles-mêmes varier en retour (par exemple, l'épuisement d'un patch de nutriments, ou au contraire la mobilisation de nutriments suite à l'exsudation). Une approche de modélisation couplant la croissance d'un système racinaire et les interactions racines sol permettrait de mettre en évidence l'émergence de synergies au sein d'un appareil racinaire, entre les portions de racines absorbantes et ou exsudantes. Sans forcément passer par une représentation explicite de l'appareil racinaire, cette question pourrait également être abordée par des modèles utilisant des représentations continues de la biomasse racinaire (Dupuy et al., 2010).

Un troisième enjeu est d'arriver à **estimer le résultat à long terme et à l'échelle de la plante entière, de la population voire de la communauté de plantes, de l'articulation de processus agissant à des échelles spatiales et temporelles variables** : l'action immédiate des racines, le dépôt et la décomposition de la litière, les effets micro-climatiques *etc.* (*Cf.* figure 1.1). La prise en compte de chacun des effets peut amener à une représentation mathématique simplifiée des interactions plantes-sol (Wu et al., 1985) qui peut être mise en valeur ensuite dans des modèles centrés sur les individus (Bittebiere et al., 2011; Grimm et al., 2006). Ce type d'approche peut mener à une meilleure compréhension des effets de patrons d'exploration dans la compétition avec d'autres plantes (*Cf.* paragraphe 5.2.3).

Enfin, un point important est de voir **comment s'articulent la capacité des plantes à**

créer des hétérogénéités de stock ou flux de nutriments et leur adaptation à des hétérogénéités préexistantes (Hodge, 2004). Dans cette étude, nous n'avons considéré que le premier cas, tandis que les études sur les stratégies d'exploration racinaire ne considèrent généralement que le second. Les études sur le terrain permettent de corréler les distributions racinaires et hétérogénéités de nutriments, mais plus rarement de distinguer les deux effets Barot et al. (1999).

5.1.3. Confrontation aux plantes "réelles"

En terme de plantes concrètes, **je me suis principalement intéressé au cours de cette thèse aux Poacées pérennes tropicales**. Outre le fait qu'elles aient été l'objet de mon étude de terrain (chapitre 3), elles ont servi à la paramétrisation de mes modèles des chapitre 2 et 4. Elles étaient un modèle biologique intéressant dans le cadre de cette thèse, par le fait que leur zone d'influence souterraine peut être représentée de manière simple. **Mon approche est cependant généralisable à d'autres cas** : l'articulation des différentes échelles d'interaction des racines avec le sol à l'échelle de la rhizosphère concerne *a priori* toutes les plantes et la prise en compte d'interactions plantes-sol à plus grande échelle doit pouvoir s'appliquer à la plupart des pérennes. Cependant, dans le cadre de l'étude des espèces arborescentes, leur capacité à développer des racines sur de grandes distances et à de grandes profondeurs rend plus difficile la caractérisation de la forme de la zone d'influence souterraine (Mordelet et al., 1996; Guevara et al., 2009; Hartle et al., 2006).

Mes hypothèses sur les interactions plante-sol à l'échelle de la rhizosphère n'ont pas pu être abordées par une approche empirique au cours de cette thèse. Pour atteindre cet objectif il faudrait mettre en œuvre des techniques très élaborées. Il existe des approches de mesures de terrain ou de laboratoire permettant de distinguer *in situ* les propriétés du sol hors et dans la rhizosphère (Herman et al., 2006), voire d'observer l'évolution temporelle de rhizosphères (Pierret et al., 2003; Hinsinger et al., 2009). Outre la question de la confrontation de la théorie aux données empiriques (*Cf.* paragraphe 5.1.1 plus haut), la mesure *in situ* de rhizosphère pourrait permettre des plans d'échantillonnage plus fins ("rhizosphère "*vs.* "bulk") et ainsi mieux découpler les effets liés à la présence de litière aérienne ou à l'action directe des racines, par exemple, sur le δ^{15}N.

Mon travail de terrain m'a permis de comparer les patrons d'exploration souterraine de trois espèces de Poacées pérennes, de comparer les propriétés du sol en fonction du degré de densité racinaire. L'usage des isotopes de l'azote a permis de comparer l'influence de chaque espèce sur le cycle de l'azote. Nos résultats suggèrent un cycle de l'azote plus rapide chez *C. dacty-*

lon que chez les cespiteuses, tandis que ces dernières seraient plus conservatrices. Cela indique un cas particulier de compromis général entre stratégies d'acquisition ou de conservation des ressources (Díaz et al., 2004). La confrontation au terrain a permis également d'intégrer aux stratégies d'exploration l'interaction des plantes avec les herbivores. On pourrait considérer que la plantes "contrôlent" les herbivores et que son appétence d'une plante est une composante d'une stratégie d'acquisition des nutriments (de Mazancourt and Loreau, 2000). Si oui, est-elle associée à une stratégie d'exploration du sol particulière ? D'autre part, on peut se demander dans quelle mesure les herbivores affectent l'efficacité des plantes contrôlant le cycle de l'azote, en inhibant la nitrification par exemple.

Un modèle d'étude pour lequel les concepts et hypothèses de cette thèse pourraient être développée est le cas général des plantes clonales. Celles-ci interagissent aussi à long terme avec le sol, et présentent diverses stratégies d'exploration, selon l'organisation de leurs unités fonctionnelles (Harper, 1980, 1977). Un avantage certain est que leurs stratégies d'exploration sont également l'objet de méthodes de modélisation éprouvées (Oborny et al., 2012; Oborny and Englert, 2012).

5.1.4. Le compromis exploration/occupation : un outil heuristique pertinent ?

Le compromis entre exploration et occupation a été formulé en introduction comme une hypothèse générale, qui a été déclinée de différentes manières dans chacun des chapitres de cette thèse. **Si l'exploration est une notion sans ambiguïté, celle d'occupation recouvre plusieurs sens selon le système, les processus considérés et les contraintes auxquelles les plantes sont soumises.** Le contrôle peut désigner le simple fait de **favoriser la disponibilité d'une ressource** – par exemple, l'exsudation de citrate qui augmente la mise en disponibilité du phosphore (Hinsinger, 2001) –, **l'efficacité de l'exploitation de cette ressource** – par exemple, en minimisant les pertes – ou une **influence générale sur la dynamique du cycle d'un nutriment** – comme le fait de favoriser un recyclage rapide des nutriments. Dans un cadre de compétition, l'occupation implique en plus une dimension de **préemption des nutriments**. L'avantage de la polysémie du terme d'occupation est qu'il permet de recouvrir dans un même cadre théorique une grande diversité de processus. L'inconvénient est de potentiellement créer une confusion, si le processus de contrôle considéré n'est pas assez explicité.

L'occupation comme l'accès à un réservoir de nutriments non directement disponible est abordée dans le chapitre 4, par un comportement de "*mining*" vis-à-vis du phosphore. Dans ce cas, la capacité des plantes à occuper le sol est exprimé par l'efficacité de l'absorption du phosphore.

A l'échelle de la plante entière, cette variable n'a été que peu affectée par la taille de la zone d'influence racinaire, mais était en revanche positivement influencée par l'hétérogénéité de la distribution racinaire. **Dans ce cadre théorique, l'occupation est donc maximisée par un système racinaire hétérogène, mais pas nécessairement plus restreint.** Cette première définition ne considère pas le recyclage d'une ressource ni son exploitation à long terme.

Une deuxième définition de l'occupation décrite de manière théorique dans les chapitres 2 et 4 est l'efficacité de l'exploitation des ressources, c'est-à dire la minimisation des pertes. Celle-ci est rendue possible à la fois par l'exploitation des nutriments perdus par la mortalité (*e.g.* les racines mortes) et par la minimisation des pertes des nutriments disponibles. Dans ce cas-là, la proximité spatiale entre le lieu de mise en disponibilité des nutriments et la racine absorbante joue un rôle important. Ce raisonnement est aussi applicable à la proximité entre racines mortes et vivantes (Abbadie et al., 1992, 2006). Dans le chapitre 4, la concentration spatiale du système racinaire minimisait les pertes de nutriments au cours du processus d'exploitation, ce qui va bien dans le sens d'un compromis exploration/occupation. On peut également noter que les systèmes exsudant le moins étaient également les plus efficaces. Cela souligne encore la distinction entre la vitesse de recyclage et le degré de fermeture des cycles de nutriments. Dans le chapitre 2, le raisonnement tenait principalement au calcul du degré de fermeture du cycle.

Les chapitres 2 et 3 nous ont également permis de **définir l'occupation comme la mise en place d'une dynamique efficace de nutriments, dans une interaction plante-sol à long-terme**. Cela implique notamment un renouvellement des ressources, *via* le dépôt de litière. Une dynamique durable peut s'installer où les stratégies d'exploration racinaires peuvent être impliquées, dans une dégradation efficace de la litière (Abbadie et al., 1992). Le terrain a posé le problème du choix des variables à mesurer pour expliciter concrètement des notions d'occupation et d'exploration du sol, et leurs relations. Une question ainsi soulevée par cette étude est de savoir si le contrôle efficace des flux de nutriment mène nécessairement à la formation d'un îlot de fertilité (accumulation de carbone et de nutriments sous les plantes). Dans l'autre sens, dans quelle mesure la formation d'un îlot de nutriment est-elle plus qu'un produit indirect du patron d'exploration et est bien liée à une stratégie explicite de contrôle du recyclage des nutriments ? L'accumulation de litière sous la canopée (Scholes and Archer, 1997) peut être vue comme la formation d'une réserve de ressource dans un environnement incertain mais l'îlot de fertilité peut bénéficier à d'autres espèce par "nursing effect" (Armas and Pugnaire, 2011), ce qui augmente potentiellement la compétition (cf paragraphe 5.2.3 ci-dessous). L'exemple de *Cynodon dactylon* suggère que les herbivores peuvent faire partie d'une stratégie de contrôle du recyclage des nutriments. En ce

cas, il feraient exception à l'hypothèse d'un compromis entre exploration et occupation. Alors que le contrôle des ressources par les microorganismes est localisé dans la rhizosphère, les grands herbivores tendent à redistribuer les ressources de manière plus uniforme. Cet effet est bien sûr dépendant aussi de la capacité de charge du système en herbivore (de Mazancourt et al., 1998). Le compromis entre exploration et occupation peut être donc généralisé à encore d'autres cas.

5.2. Généralisation : stratégies d'acquisition des ressources et rétroactions plante-sol

5.2.1. Un autre mode d'acquisition des ressources : les associations mycorhiziennes

Je n'ai discuté explicitement au cours de cette thèse que du cas de l'exploration racinaire. Or, la grande majorité des plantes explorent également le sol par l'investissement dans les symbioses mycorhiziennes (Whitfield, 2007; Croft et al., 2011). Celles-ci compliquent l'application de mes hypothèses de travail de deux manières.

A échelle fine, **l'approche mécaniste développée dans le chapitre 4 pourrait être appliquée à l'exploration par les hyphes** (Agerer, 2001). Comme les racines, celles-ci libèrent dans le sol des substances telles que les acides organiques, qui favorisent la mobilisation de ressources, qu'ils absorbent dans un second temps (Pritsch and Garbaye, 2011). Les échelles de temps et d'espaces de ces processus restent à estimer et la finesse et le *turnover* important des hyphes rend difficile leur observation *in situ*.

L'exploration indirecte du sol pour les plantes permise par les champignons mycorhiziens remet en question le raisonnement à l'origine de l'hypothèse du compromis entre exploration et occupation. Celui-ci peut être résumé par la question de l'accès à différents pools de nutriments : en investissant localement dans l'exsudation et la prolifération de racines une plante accède à un pool de ressource (les nutriments non disponibles) auquel elle n'aurait pas accès en allouant ses racines et ses exsudats dans un volume de sol plus grand. En ne considérant que l'exploration racinaire, le compromis repose sur une question d'allocation de racines dans l'espace. Dans le cas des mycorhizes, la part de matière et d'énergie qu'une plante investit dans la symbiose la restreint dans sa capacité à construire des racines et à explorer et influencer le sol par elle-même (Landeweert and Hoffland, 2001). Cela est aussi vrai pour l'investissement d'énergie dans d'autres symbioses, comme celles des nodules de fixation de l'azote atmosphérique. Cependant, les hyphes des champignons mycorhiziens développent une surface d'interaction avec le sol bien plus grande à biomasses équivalentes (Agerer, 2001). Ainsi, une plante contrôlant son accès aux nutriments

par le biais de mycorhizes limite sa surface directe avec le sol, mais augmente considérablement sa surface d'interaction indirecte.

5.2.2. Spécificité des interactions entre les plantes et les microorganismes du sol

Au delà des mycorhizes, par les différents mécanismes d'interaction avec le sol, les plantes favorisent passivement ou activement la présence d'une communauté microbienne spécifique Muci et al. (2012); Haichar et al. (2014). Une part de cette spécificité repose sur la capacité des microorganismes à dégrader la litière ou les exsudats de la plante à laquelle ils sont associés (Ayres et al., 2009). Ce type de mécanisme tendrait à favoriser des plantes au comportement territorial (Schenk et al., 1999). Un autre cas de relation spécifique entre plante et microorganismes est le cas des pathogènes. Dans certaines expériences mesurant l'effet d'héritage, des plantes sont défavorisées en poussant sur le sol occupé par la même espèce auparavant, par comparaison avec des sols occupés auparavant par d'autres espèces (Hendriks et al., 2013). Cela invite à considérer les racines mortes, non plus comme des potentielles sources de nutriments, mais comme des agents de transmissions de pathogène. Cette rétroaction négative a des conséquences potentielles sur les stratégies d'exploration, à l'encontre de mes hypothèses. Elle conduirait à des comportements où les plantes font pousser leur racine pour minimiser le contact potentiel avec d'anciennes rhizosphères ou racines mortes, qui portent potentiellement des pathogènes (Hodge et al., 2009). En vue d'applications concrète, ce point invite à considérer les stratégies d'exploration des plantes dans le cadre plus général des rétroactions plantes-sol (Ehrenfeld et al., 2005).

5.2.3. Les rétroactions plantes-sol à l'échelle de la communauté de plantes

Une autre limitation méthodologique de cette thèse a été de ne considérer que des plantes seules ou en population, ce qui nous a permis notamment de mettre de côté la question de la compétition. Dans une certaine mesure, cette simplification peut se justifier par le fait de considérer des plantes dont le système racinaire est localement dense et dans des écosystèmes pauvres en nutriments. Cependant, **la portée générale du travail de cette thèse dépend de l'application de mes hypothèses de travail aux interactions entre espèces de plante**.

A l'échelle de la rhizosphère, la prise en compte des différents rayons d'action des racines (chapitre 4) complique la compréhension de la compétition entre plantes (Raynaud et al., 2008). Classiquement, la compétition souterraine entre plantes est considérée comme symétrique : le partage des ressources se fait en fonction de la proportion de longueur racinaire de chacun

des compétiteurs (Huston and DeAngelis, 1994). Cependant, des cas théoriques de compétition asymétrique ont été montrés en mettant en présence deux plantes différant dans leur taux d'absorption (Raynaud and Leadley, 2005; Rewald and Leuschner, 2009). De la même manière, différents niveaux de taux d'exsudation pourraient mener à une compétition asymétrique. Sur le plan méthodologique, la mesure des rhizosphères comme je l'ai fait au chapitre 4 ne suffit sans doute pas pour aider à bien comprendre le fonctionnement d'un volume de sol occupé par deux plantes en compétition. Le découpage du sol en polyhèdres de Thiessen (Comerford et al., 1994; Raynaud and Leadley, 2004; Berger et al., 2008) est un autre outil utilisable dans ce contexte.

La notion d'occupation peut donc être reformulée dans un contexte de compétition. Comme déjà évoqué, l'application de la métaphore "guérilla contre phalange" aux plantes est une des dimensions possibles de l'hypothèse d'un compromis exploration/occupation. Cette métaphore fait appel à la préemption des nutriments : en gardant un système racinaire dense, une plante s'assure que les ressources présentes dans sa zone d'exploration ne seront pas absorbées par un compétiteur (Harper, 1980). Bien que nous n'ayons pas considéré la compétition entre plantes, cette dimension de compétition par consommation était présente dans le rôle des pertes au chapitre 4. Il est aussi possible d'appliquer le compromis exploration/occupation à la compétition par interférence (*i.e.* par interaction directe avec le compétiteur). Une plante inhibant par allélopathie la croissance d'autres plantes ou de microorganismes y investit une quantité importante de matière et d'énergie (Marschner, 1995). Il est possible que de telles stratégies soient dépendantes de comportements racinaires précis : par exemple, si un système racinaire dilué dans un grand volume ne peut efficacement inhiber la croissance de compétiteurs. On retrouverait dans ce cas un compromis exploration/occupation.

La facilitation est un autre mode d'interactions entre espèces à considérer (Tewksbury and Lloyd, 2001; Pugnaire et al., 1996; Holmgren et al., 1997). A l'échelle de la rhizosphère, le fait que les racines puissent augmenter la disponibilité des ressources sur un volume plus large que celui dans lequel elles abaissent le volume des ressources peut bénéficier à des racines voisines d'autres plantes. A l'inverse de comportements territoriaux (Schenk et al., 1999), certains assemblages végétaux mènent à des interactions locales de différentes plantes. Cela va de l'interaction de clones plus ou moins intégrés physiologiquement (Derner and Briske, 1998), aux touffes plurispécifiques ou au bosquets (Abbadie et al., 2006). Dans le cas emblématique des brousses tigrées, une limitation de l'exploration s'observe à l'échelle de la communauté entière, liée aux contraintes en eau (White, 1970). Que ce soit à l'échelle de la plante individuelle ou de la communauté de plantes, le même problème se pose de savoir comment les patrons optimaux

prédits par la théorie peuvent émerger effectivement, au cours du développement racinaire ou par la dynamique des communautés (Kéfi et al., 2008, 2007).

5.2.4. Application aux agro-écosystèmes ?

Comme évoqué dans l'introduction du chapitre 1, **l'étude du fonctionnement des systèmes plante-sol en milieu naturel est une source potentielle d'inspiration pour la mise en place de méthodes agricoles plus durables** (Malézieux, 2011). Différents axes de recherche sont possibles selon que l'on place au centre du raisonnement la plante ou la population de plante cultivées (*e.g.* Weiner et al. 2010) ou bien le système plantes-sol dans son ensemble (Vitousek et al., 1997). Dans le premier cas, l'accent est mis sur la performance des plantes en terme de productivité tandis que dans le second, la durabilité du système est au centre du raisonnement, avec pour but le maintient des propriétés du sol et la limitation des impacts en aval, par des systèmes plus conservatifs en azote (Subbarao et al., 2010).

Un enjeu important en agriculture est la sélection de traits d'intérêt pour les plantes cultivées(White et al., 2013). Au cours de cette thèse, je me suis principalement intéressé à des traits d'ensemble de l'appareil racinaire, notamment l'étendue horizontale de la zone d'influence souterraine. Une meilleure compréhension du déterminisme génétique et physiologique du développement racinaire (*e.g.* Forde 2014) rendraient possible la sélection de plantes restreignant leur domaine d'exploration. Un exemple précis est la sensibilité du gravitropisme, qui détermine l'étalement horizontal de l'appareil racinaire de certaines espèces (Rubio et al., 2001).

Comme discuté plus haut, le principal objet d'application de ma thèse a été le cas des Poacées pérennes et en particulier les cespiteuses. Une hypothèse générale par rapport à celles-ci est que leur forme de croissance favorise le contrôle des cycles de nutriments, par exemple *via* l'inhibition biologique de la nitrification (Subbarao et al., 2013) et de cycles de nutriments plus fermés, en particulier pour l'azote. Ces hypothèses peuvent être appliquées aux tentatives de domestication et de culture d'herbe pérennes, pour la production de graines (Cox et al., 2006; Glover et al., 2007). Une application plus directe est la gestion des prairies pâturées par le bétail, en particulier en milieux tropicaux où des cespiteuses constituent une part importante du fourrage et contrôlent fortement le cycle de l'azote (Subbarao and Rao, 2013). Comme développés au chapitre 3, les herbivores tendent à favoriser la minéralisation et la nitrification (Frank et al., 2000). Une meilleure compréhension du cycle de l'azote dans les systèmes sol-plantes-herbivores devrait donc mener à des perspectives de gestion intéressantes. Par exemple, pour maintenir une densité de bétail optimale pour le maintien d'un sol riche en carbone et en azote.

L'action de l'homme sur les agrosystèmes a des propriétés analogues à celle des grands herbivores sur les systèmes plante-sol : il exporte la biomasse et des nutriments par la récolte et apporte des nutriments immédiatement disponibles par les engrais. Dans le cadre de mon étude de terrain (chapitre 3), je formule l'hypothèse que accès à des ressources disponible par un recyclage par les herbivores a un coût en terme de fermeture du cycle des nutriments, notamment par le fait que les grands herbivores redistribuent les nutriments de manière relativement uniforme (en considérant des temps longs). Ce compromis pourrait être dépassé dans le cadre des agro-écosystèmes, par une répartition hétérogène des fertilisants, en fonction de la distribution du couvert végétal.

5.3. Conclusion

Cette thèse a permis de discuter des **relations entre structure et fonctionnement des systèmes plante-sol**, autour de la question du cycle des nutriments limitants. La principale originalité de ce travail a consisté à proposer d'**articuler différentes échelles des interactions plantes-sol**. A **échelle fine**, j'ai montré que la **prise en compte de différentes tailles de rhizosphères**, selon les conditions et le processus considérés, élargissait la compréhension des interactions entre racines appartenant à un même système racinaire. A l'**échelle de la plante entière et de la population de plante**, j'ai proposé que l'**intégration des différents processus d'interaction plante-sol mène** à un compromis entre l'échelle d'exploration du sol par les plantes et leur capacité d'influence des processus du sol. J'ai proposé l'usage du compromis exploration-occupation comme hypothèse heuristique générale, que j'ai pu développer sous différents angles tout en proposant d'autres approches possibles.

L'apport principal de cette thèse à l'étude des stratégies d'exploration racinaire est de considérer l'action des racines à la fois comme organes de préemption des nutriments (Cahill and McNickle, 2011), mais surtout comme organes de modification du sol, et d'interaction avec d'autres processus comme le dépôt de litière. Un autre point important a été de tenter de caractériser et d'articuler les différentes échelles de ces processus. En retour, cette approche permet d'éclairer la compréhension des rétroactions plantes-sol, notamment le compromis entre vitesse et fermeture des cycles de nutriments. En outre, cela souligne d'autant plus la capacité des plantes à créer des hétérogénéités dans le fonctionnement du sol, montrant la complexité de leur rôle d'ingénieur des écosystèmes Jones et al. (1994); Van Breemen and Finzi (1998).

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Cinquième partie .

Annexes

6. Appendix to Chapter 2

6.1. Equations and stability conditions for model 2

6.1.1. Model description

Following Levins (1969) we define μ and c as parameters for reduction and increase in plant occupation, respectively. For example, when all the roots in a given volume of soil die, this volume becomes unoccupied and plant material and detritus contained in it are added to the D_U compartment. We suppose soil exploration x to be constant. This implies that losses of soil volumes are always compensated by colonization:

$$\frac{dx}{dt} = c\,x\,(1-x) - \mu\,x \tag{6.1}$$

If $x \neq 0$, this leads to $\mu = c\,(1-x)$, which allows us to use μ as an indicator of the intensity of fluxes between occupied or unoccupied soil.

There are four lateral fluxes from P_O and D_O to D_U, from N_O to N_U, from D_U to D_O and from N_U to N_O (figure 2.2 in the main text). For an easier comparison of the system properties for different values of μ, we suppose that plant mortality (d_P) is not affected by these dynamics: whatever the value of μ, P_O output equals $(d_P + l_P)\,P_O$. From the flux $d_P\,P_O$, $\mu\,x\,P_O$ goes to D_U and $(d_P - mu\,x)\,P_O$ goes to D_O (figure 2.2). Thus we must have: $\mu\,x < d_P$.

The equations for the second model are:

$$\frac{dP_O}{dt} = u_N\,N_O\,P_O - (d_P + l_P)P_O \tag{6.2}$$

$$\frac{dD_O}{dt} = r_D + (d_P - \mu\,x)\,P_O + \mu\,x\,D_U + (m_D + l_D + \mu\,x)\,D_O$$

$$\frac{dN_O}{dt} = r_N + m_D\,D_O + \mu\,x\,N_U - (u_N\,P_O + l_N + \mu\,x)N_O$$

$$\frac{dD_U}{dt} = r_D + \mu\,x\,(P_O + D_O) - (m_D + l_D + \mu\,x)D_U$$

$$\frac{dN_U}{dt} = r_N + m_D\,D_U + \mu\,x\,N_O - (l_N + \mu\,x)\,N_U$$

6.1.2. Stability of the equilibrium

The equilibrium values for model 2 are the following:

$D_O^* = \frac{1}{m_D u_N(m_D x\alpha_D\alpha_P\mu(-l_N+x\mu)+d_P(x^2\alpha_D^2\alpha_P\mu^2+l_N(m_D(-1+\alpha_D\alpha_P)+x\alpha_D(-2+\alpha_D\alpha_P)\mu)))}(\alpha_D(d_P^2 l_N(l_N + x\mu)(m_D + x\alpha_D\mu) + m_D u_N x\alpha_P\mu(l_N r_N + x(r_N + 2r_D\alpha_D)\mu) - d_P(l_N^2 m_D x\mu + u_N x\alpha_P\mu(m_D(r_N + r_D\alpha_D) + r_N x\alpha_D\mu) + l_N(u_N x\alpha_D(2r_D + r_N\alpha_P)\mu + m_D(r_D u_N + r_N u_N\alpha_P + x^2\mu^2)))))$

$P_O^* = \frac{(d_P l_N - u_N(r_N+r_D\alpha_D)\alpha_P)(l_N+x\mu)(m_D+2x\alpha_D\mu)}{u_N(m_D x\alpha_D\alpha_P\mu(-l_N+x\mu)+d_P(x^2\alpha_D^2\alpha_P\mu^2+l_N(m_D(-1+\alpha_D\alpha_P)+x\alpha_D(-2+\alpha_D\alpha_P)\mu)))}$

$N_O^* = \frac{d_P}{u_N\alpha_P}$

$D_U^* = \frac{1}{m_D u_N(m_D x\alpha_D\alpha_P\mu(-l_N+x\mu)+d_P(x^2\alpha_D^2\alpha_P\mu^2+l_N(m_D(-1+\alpha_D\alpha_P)+x\alpha_D(-2+\alpha_D\alpha_P)\mu)))}(\alpha_D(d_P^2 l_N x\alpha_D\mu(l_N + x\mu) - m_D u_N x\alpha_P\mu(l_N(r_N + 2rd\alpha_D) + r_N x\mu) + d_P(l_N^2 m_D x\mu - r_N u_N x^2\alpha_D\alpha_P\mu^2 + l_N(-u_N x\alpha_D(2rd + r_N\alpha_P)\mu + m_D(rd u_N(-1 + \alpha_D\alpha_P) + x^2\mu^2)))))$

$N_U^* = \frac{1}{u_N(m_D x\alpha_D\alpha_P\mu(-l_N+x\mu)+d_P(x^2\alpha_D^2\alpha_P\mu^2+l_N(m_D(-1+\alpha_D\alpha_P)+x\alpha_D(-2+\alpha_D\alpha_P)\mu)))}(-2m_D u_N x\alpha_D(r_N + r_D\alpha_D)\alpha_P\mu + d_P^2 x\alpha_D^2\mu(l_N + x\mu) + d_P(-2u_N x\alpha_D(r_N + r_D\alpha_D)\mu + m_D(r_N u_N(-1 + \alpha_D\alpha_P) + \alpha_D(r_D u_N(-1 + \alpha_D\alpha_P) + x\mu(l_N + x\mu)))))$

The Jacobian for model 2 is:

$$J(P_O,D_O,N_O,D_U,N_U) = \begin{bmatrix} u_N(x)N_O - \frac{d_P}{\alpha_P} & 0 & u_N(x)P_O & 0 & 0 \\ d_{P-}\mu\,x & -(\frac{m_D}{\alpha_D} + \mu\,x) & 0 & 0 & 0 \\ -u_N(x)N_O & m_D & -u_N(x)P_O - l_N & 0 & 0 \\ \mu\,x & \mu\,x & 0 & \frac{m_D}{\alpha_D} + \mu\,x & 0 \\ 0 & 0 & \mu\,x & m_D & -(l_N + \mu\,x) \end{bmatrix} \tag{6.3}$$

Which leads to the following polynomial for $J(P_O^*, D_O^*, N_O^*, D_U^*, N_U^*)$:

$$p(\lambda) = -\lambda^5 - a_1\,\lambda^4 - a_2\,\lambda^3 - a_3\,\lambda^2 - a_4\,\lambda - a_5 \tag{6.4}$$

With:
$a_1 = 2l_N + \frac{2m_D}{\alpha_D} + 3x\mu + \frac{(d_P l_N - u_N(r_N+r_D\alpha_D)\alpha_P)(l_N+x\mu)(m_D+2x\alpha_D\mu)}{m_D x\alpha_D\alpha_P\mu(-l_N+x\mu)+d_P(x^2\alpha_D^2\alpha_P\mu^2+l_N(m_D(-1+\alpha_D\alpha_P)+x\alpha_D(-2+\alpha_D\alpha_P)\mu))}$

$$\begin{aligned} a_2 = {} & l_N^2 + \frac{m_D^2}{\alpha_D^2} + 4\frac{l_N m_D}{\alpha_D} + 5l_N x\mu + 4x\mu\frac{m_D}{\alpha_D} + 2x^2\mu^2 \\ & + \frac{l_N(d_P l_N - u_N(r_N + r_D\alpha_D)\alpha_P)(l_N + x\mu)(m_D + 2x\alpha_D\mu)}{m_D x\alpha_D\alpha_P\mu(-l_N + x\mu) + d_P(x^2\alpha_D^2\alpha_P\mu^2 + l_N(m_D(-1 + \alpha_D\alpha_P) + x\alpha_D(-2 + \alpha_D\alpha_P)\mu))} \\ & + \frac{2m_D(d_P l_N - u_N(r_N + r_D\alpha_D)\alpha_P)(l_N + x\mu)(m_D + 2x\alpha_D\mu)}{\alpha_D(m_D x\alpha_D\alpha_P\mu(-l_N + x\mu) + d_P(x^2\alpha_D^2\alpha_P\mu^2 + l_N(m_D(-1 + \alpha_D\alpha_P) + x\alpha_D(-2 + \alpha_D\alpha_P)\mu)))} \\ & + \frac{d_P(d_P l_N - u_N(r_N + r_D\alpha_D)\alpha_P)(l_N + x\mu)(m_D + 2x\alpha_D\mu)}{\alpha_P(m_D x\alpha_D\alpha_P\mu(-l_N + x\mu) + d_P(x^2\alpha_D^2\alpha_P\mu^2 + l_N(m_D(-1 + \alpha_D\alpha_P) + x\alpha_D(-2 + \alpha_D\alpha_P)\mu)))} \\ & + \frac{2x(d_P l_N - u_N(r_N + r_D\alpha_D)\alpha_P)\mu(l_N + x\mu)(m_D + 2x\alpha_D\mu)}{m_D x\alpha_D\alpha_P\mu(-l_N + x\mu) + d_P(x^2\alpha_D^2\alpha_P\mu^2 + l_N(m_D(-1 + \alpha_D\alpha_P) + x\alpha_D(-2 + \alpha_D\alpha_P)\mu))} \end{aligned}$$

$a_3 = \frac{1}{\alpha_D^2\alpha_P(m_D x\alpha_D\alpha_P\mu(-l_N+x\mu)+d_P(x^2\alpha_D^2\alpha_P\mu^2+l_N(m_D(-1+\alpha_D\alpha_P)+x\alpha_D(-2+\alpha_D\alpha_P)\mu)))}(d_P^2 l_N\alpha_D(l_N + x\mu)(m_D + 2x\alpha_D\mu)(m_D(2 - \alpha_D\alpha_P) + \alpha_D(l_N + 2x\mu)) - \alpha_P^2 left(2l_N^3 m_D x\alpha_D^2\mu(m_D + x\alpha_D\mu) + 2l_N^2\alpha_D(m_D + 2x\alpha_D\mu)(m_D u_N(r_N + r_D\alpha_D) + m_D^2 x\mu + u_N x\alpha_D(r_N + r_D\alpha_D)\mu) + m_D x\mu(m_D + 2x\alpha_D\mu)(u_N x\alpha_D(2+\alpha_D)(r_N + r_D\alpha_D)\mu + m_D(r_N u_N + r_D u_N\alpha_D - x^2\alpha_D\mu^2)) + l_N(4u_N x^3\alpha_D^3(r_N +$

$r_D\alpha_D)\mu^3 + m_D^3(r_N u_N + r_D u_N \alpha_D - x^2\alpha_D\mu^2) + m_D^2 x\alpha_D\mu(r_N u_N(6+\alpha_D) + \alpha_D(r_D u_N(6+\alpha_D) - 4x^2\mu^2)) + 2m_D x^2\alpha_D^2\mu^2(r_N u_N(5+\alpha_D) + \alpha_D(r_D u_N(5+\alpha_D) - x^2\mu^2)))) + d_P\alpha_P(2l_N^3\alpha_D^2\alpha_P(m_D + x\alpha_D\mu)^2 + l_N^2(m_D + 2x\alpha_D\mu)(m_D^2(-1+2\alpha_D\alpha_P) + m_D x\alpha_D(-2+\alpha_D+4\alpha_D\alpha_P)\mu - \alpha_D^2(r_N u_N + r_D u_N\alpha_D - 2x^2\alpha_D\alpha_P\mu^2)) + x\alpha_D\mu(m_D + 2x\alpha_D\mu)(-2u_N x\alpha_D(r_N + r_D\alpha_D)\mu + m_D(r_N u_N(-2+\alpha_D\alpha_P) + \alpha_D(r_D u_N(-2+\alpha_D\alpha_P) + x^2\alpha_P\mu^2))) + l_N\alpha_D left(m_D^3 x\alpha_P\mu + 2x^2\alpha_D^2\mu^2(-3r_N u_N - 3r_D u_N\alpha_D + x^2\alpha_D\alpha_P\mu^2) + m_D x\alpha_D\mu(r_N u_N(-7+2\alpha_D\alpha_P) + \alpha_D(r_D u_N(-7+2\alpha_D\alpha_P) + 2x^2(1+4\alpha_P)\mu^2)) + m_D^2(r_N u_N(-2+\alpha_D\alpha_P) + \alpha_D(r_D u_N(-2+\alpha_D\alpha_P) + x^2(1+5\alpha_P)\mu^2)))))$

$a_4 = -\frac{(l_N+x\mu)(m_D+2x\alpha_D\mu)}{\alpha_D^2\alpha_P(m_D x\alpha_D\alpha_P\mu(-l_N+x\mu)+d_P(x^2\alpha_D^2\alpha_P\mu^2+l_N(m_D(-1+\alpha_D\alpha_P)+x\alpha_D(-2+\alpha_D\alpha_P)\mu)))}(d_P^2 l_N(m_D^2(-1+\alpha_D\alpha_P) - 2l_N x\alpha_D^2\mu + m_D\alpha_D(-2+\alpha_D\alpha_P)(l_N+x\mu)) + \alpha_P^2 m_D(l_N(m_D(\alpha_D r_D u_N + r_N u_N + \alpha_D\mu^2(-x^2)) + \alpha_D(\alpha_D+2)\mu u_N x(\alpha_D r_D + r_N)) + \alpha_D\mu u_N x(\alpha_D r_D + r_N)(m_D - \alpha_D\mu x) + \alpha_D\mu m_D x l_N^2) - d_P\alpha_P(-2l_N u_N x\alpha_D^2(r_N + r_D\alpha_D)\mu + m_D^2(r_N u_N(-1+\alpha_D\alpha_P) + \alpha_D(r_D u_N(-1+\alpha_D\alpha_P) + l_N(l_N\alpha_P + x\mu))) + m_D\alpha_D(l_N^2 x\alpha_D(1+\alpha_P)\mu + u_N x(r_N + r_D\alpha_D)(-2+\alpha_D\alpha_P)\mu) + l_N(r_N u_N(\alpha_D\alpha_P - 2) + \alpha_D(r_D u_N(\alpha_D\alpha_P - 2) + x^2(-1+\alpha_P)\mu^2))))$

$a_5 = \frac{m_D}{\alpha_D^2\alpha_P}(-d_P l_N + u_N(r_N + r_D\alpha_D)\alpha_P)(l_N + x\mu)(m_D + 2x\alpha_D\mu)$

The Rout Hurwitz criteria in this case are the following:

$$a_i > 0,\ \forall i \in \{1...5\} \tag{6.5}$$

$$a_1\, a_2\, a_3 > a_3^2 + a_1^2\, a_4$$

$$(a_1\, a_4 - a_5)(a_1\, a_2\, a_3 - a_3^2 - a_1^2 a_4) > a_5(a_1\, a_2 - a_3)^2 + a_1 a_5^2$$

We found that our equilibrium is stable when the fluxes are not too strong. We checked numerically that it was the case for the numerical cases presented in the main part of the article.

6.2. Trade-offs equations and parameterization of the model

6.2.1. Trade-off equations

Table 6.1.: trade-offs tested in the analysis of the model

type of trade-off	equation
linear	$u_N(x) = u_N^1\,(1 + \beta_{UN}\,(1-x))$
convex	$u_N(x) = u_N^1/x$
	$u_N(x) = u_N^0\,(1 - \beta_{UN}\,x)^2$
	$u_N(x) = u_N^1\,(1 + \beta_{UN}\,(1-x))^2$
	$u_N(x) = u_N^1\,(1 + \beta_{UN}\,(1-x)^2)$
concave	$u_N(x) = u_N^1\,\sqrt{1 + \beta_{UN}\,(1-x)}$
	$u_N(x) = u_N^1\,(1 + \beta_{UN}\,\sqrt{1-x})$

6.2.2. Parameterization

The parameters for Lamto ecosystem were calculated using Abbadie et al. (2006). Mineral and organic nitrogen inputs by dry and wet deposition were estimated as 14.6 and 14.0 kg N.

$ha^{-1}.yr^{-1}$ respectively. Soil mineral and organic losses by leaching reached 0.2 and 5.0 kg $N.ha^{-1}.yr^{-1}$ respectively. Annual fire induces a flux from plant biomass to the atmosphere of 9 to 24 kg $N.ha^{-1}.yr^{-1}$. We fixed it to 23.4 kg $N.ha^{-1}.yr^{-1}$ to balance inputs and outputs in the system. Plant annual requirements in nitrogen reach 80 kg $N.ha^{-1}.yr^{-1}$. We neglected nitrogen fixation, which is negligible in the system, to keep the general formulation of our model. If we consider the plant compartment to be at equilibrium, we have a flux from the plant to the detritus compartment of 56.6 kg $N.ha^{-1}.yr^{-1}$. Mineralization rate was estimated as 65.6 kg $N.ha^{-1}.yr^{-1}$ to balance fluxes to and from the detritus compartment. Grass total nitrogen stock and soil organic content were estimated at 54 and 2800 kg $N.ha^{-1}$ respectively. Soil mineral content is more difficult to estimate, so we used the approximation of de Mazancourt et al. (1999) of a mineral nitrogen stock of 2 kg $N.ha^{-1}$. We also parametrized nitrogen cycling for a British upland pasture using data from Batey (1982). From those data, plant compartment was fixed at 100 kg N. ha^{-1} and soil organic matter at 6250 kg N. ha^{-1}. As no data on mineral nitrogen was available, we fixed it at 32 kg $N.ha^{-1}$, which corresponds to 0.51 % of soil total nitrogen. We fixed system losses at 5 kg N.ha-1 for plant losses, 4 kg $N.ha^{-1}$ for mineral and 5 kg $N.ha^{-1}$ for organic losses. The values chosen for mineralization and plant uptake from field data were: 40 kg N. $ha^{-1}.yr^{-1}$ and 43 kg $N.ha^{-1}.yr^{-1}$ respectively. No data was available for the flux between the plant and the detritus compartment. We therefore fixed it at 38 kg $N.ha^{-1}.yr^{-1}$ to balance fluxes in the system. All these parameter values are summarized in table 6.2.

Table 6.2.: Parameters values in the two cases considered in our study.

Parameters	Lamto savannas	British upland
r_D	14	7
r_N	14.6	7
l_P	0.43	0.005
l_D	0.001	0.0008
l_N	0.1	0.125
u_N	0.74	0.0134
d_P	1.05	0.38
m_D	0.023	0.0064

6.2.3. trade-off calibration

To calibrate our trade-offs, we chose reference values for soil exploration in the system, based on the supposed pattern of roots. This reference value was set for 1 in the British upland where the soil is completely explored by roots and 0.3 for Lamto savannas. This last figure was

estimated from data of root distribution (Menaut and Abbadie, 2006).

6.3. Detailed analysis of model 1 with a functional trade-off between exploration and uptake

6.3.1. Stability conditions

In the first model, the zone of influence and the unexplored soil are systems that can be analyzed independently. We can thus calculate the Jacobian matrix for the zone of influence J_O, using equations 2.3.

$$J_O(P_O, D_O, N_O) = \begin{bmatrix} u_N(x)\, N_O - \frac{d_P}{\alpha_P} & 0 & u_N(x)\, P_O \\ d_P & -\frac{m_D}{\alpha_D} & 0 \\ -u_N(x)\, N_O & m_D & -u_N(x)\, P_O - l_N \end{bmatrix} \tag{6.6}$$

We then calculate the characteristic polynomial of :$J_O(P_O^*, D_O^*, N_O^*)$:

$$p(\lambda) = -\lambda^3 - a_1\lambda^2 - a_2\lambda - a_3 \tag{6.7}$$

With

$$\begin{aligned} a_1 &= \frac{\alpha_P\, u_N(x)(\alpha_D\, r_D + r_N) - d_P\, l_N}{d_P(1 - \alpha_P\, \alpha_D)} + \frac{m_D}{\alpha_D} + l_N \\ &= u_N\, P_O + \frac{m_D}{\alpha_D} + l_N \\ &= l_N(R + \frac{\alpha_P\, \alpha_D}{1 - \alpha_P\, \alpha_D}) + \frac{m_D}{\alpha_D} \end{aligned} \tag{6.8}$$

$$\begin{aligned} a_2 &= \frac{\alpha_P u_N(x)(\alpha_D r_D + r_N)(\alpha_D d_P + \alpha_P m_D) - \alpha_D d_P l_N(d_P + \alpha_P r^2 m_D)}{\alpha_D\, \alpha_P\, d_P(1 - \alpha_P\, \alpha_D)} \\ &= l_N \frac{\alpha_D\, d_P\, (R-1) + \alpha_P\, m_D\, (R - \alpha_D\, \alpha_P)}{\alpha_D\, \alpha_P(1 - \alpha_P\, \alpha_D)} \end{aligned}$$

$$\begin{aligned} a_3 &= m_D\, \frac{\alpha_P u_N(r_N + \alpha_D r_D) - d_P l_N}{\alpha_P \alpha_D} \\ &= d_P\, l_N \frac{m_D}{\alpha_D\, \alpha_P\, (R-1)} \end{aligned}$$

According to the Routh-Hurwitz criteria, the equilibrium is stable if: (i) $a_1 > 0$, (ii) $a_3 > 0$ and (iii) $a_1 a_2 > a_3$. Conditions (i) and (ii) are always verified when the equilibrium is positive. Condition (iii) is equivalent to $A > 0$, with:

$$A = (l_N\, (R + \frac{\alpha_P \alpha_D}{1 - \alpha_P \alpha_D}) + \frac{m_D}{\alpha_D})(\alpha_D d_P\, (R-1) + \alpha_P m_D\, (R - \alpha_D \alpha_P)) - d_P m_D\, (R-1)(1 - \alpha_P \alpha_D) \tag{6.9}$$

Calculation leads to:

$$A > (\frac{m_D}{\alpha_D})(\alpha_D d_P\,(R-1) + \alpha_P m_D(R - \alpha_P\alpha_D)) - d_P m_D(R-1)(1-\alpha_P\alpha_D) \tag{6.10}$$

Which can be simplified in:

$$A > m_D\,(\alpha_P\alpha_D d_P + \frac{m_D}{\alpha_D}(R - \alpha_P\alpha_D))$$

The condition to have a positive equilibrium (main text) implies $R(x) > \alpha_P\alpha_D$ so that:

$$A > 0 \tag{6.11}$$

The conditions for stability are thus verified when every positive equilibrium is stable.

6.3.2. Calculation of optimal soil exploration x_P

We generalized the results obtained with the linear trade-off by calculating x_P for the different trade-offs between x and of $u_N(x)$. Some of the expressions tested where not mathematically tractable, but even in theses cases, a numerical value of x_P lower than 1 could be obtained numerically. Table 6.3 summarizes some of the literal expressions of x_P obtained. In all cases, restricted exploration is favoured by low values of $R(1)$ and high values of β_{UN}.

Table 6.3.: The literal expression of x_P for different expressions of $u_N\,(x)$ and the condition for it to be defined. When the literal expression of x_P was too difficult to analyse, we could at least obtained it numerically with Lamto parameters.

$u_N(x)$	x_P	Condition for $x_P < 1$
$u_N(x) = u_N^1\,(1 + \beta_{UN}\,(1-x))$	$\frac{1}{\beta_{UN}}(\beta_{UN} + 1 - \sqrt{\frac{\beta_{UN}+1}{R(1)}})$	$R(1) < 1 + \beta_{UN}$
$u_N(x) = u_N^1/x$	$\frac{R(1)}{2}$	$R(1) < 2$
$u_N(x) = u_N^0\,(1 - \beta_{UN}\,x)^2$	$\frac{1}{\beta_{UN}}(1 - (\frac{1}{R(1)})^{\frac{1}{3}})$	$R(1) < \frac{1}{(1-\beta_{UN})^3}$
$u_N(x) = u_N^1\,(1 + \beta_{UN}\,(1-x))^2$	$\frac{1-\beta_{UN}}{\beta_{UN}}(1 - (\frac{1-\beta_{UN}}{R(1)})^{\frac{1}{3}})$	$R(1) < \frac{(1-\beta_{UN})^4}{(1-2\,\beta_{UN})^3}$

6.3.3. Variation of soil nutrient stocks D^* and N^* with soil exploration x

Here we analyze the variation of D^* and N^* with x. By the use of equilibrium conditions, we get the following expressions for D^* and N^*:

$$D^*(x) = \frac{\alpha_D}{m_D}(x\,r_D + d_P\,P^*(x)) + (1-x)\alpha_D\frac{r_D}{m_D} \tag{6.12}$$

$$N^*(x) = x\frac{d_P}{\alpha_P\,u_N(x)} + (1-x)\frac{r_N + \alpha_D r_D}{l_N} \tag{6.13}$$

By the use of partial derivation, we get:

$$\frac{\partial D^*}{\partial x}(x) = d_P\frac{\alpha_D}{m_D}\frac{\partial P^*}{\partial x}(x) \tag{6.14}$$

$$\frac{\partial N^*}{\partial x}(x) = \frac{d_P}{\alpha_P}(\frac{u_N(x) - x\,u_N'(x)}{u_N^2(x)}) - \frac{r_N + \alpha_D r_D}{l_N} \tag{6.15}$$

We can deduce by the mathematical expression of P^* that:

$$\frac{\partial P^*}{\partial x}(x) = \frac{l_N}{1-\alpha_D\alpha_P}(\frac{R}{u_N(x)} - \frac{u_N(x) - x\,u'_N(x)}{u_N^2(x)}) \tag{6.16}$$

It is then obvious from equations and that P^* and D^* vary together in opposition with N^*.

6.3.4. Variation of total nutrient stocks T^* with soil exploration x

It can be shown using equation and equilibrium conditions that:

$$T^*(x) = P^*(x)(1+\alpha_D\frac{d_P}{m_D}) + (\frac{\alpha_D}{m_D}r_D + \frac{r_N+\alpha_D r_D}{l_N}) + x(\frac{d_P}{\alpha_P u_N(x)} - \frac{r_N+\alpha_D r_D}{l_N})$$

By the use of partial derivation we get:

$$\frac{\partial T^*}{\partial x}(x) = \frac{\partial P^*}{\partial x}(x)(1+\alpha_D\frac{d_P}{m_D}) - \frac{r_N+\alpha_D r_D}{l_N} + \frac{d_P}{\alpha_P u_N^2(x)}(u_N(x) - xu'_N(x)) \tag{6.17}$$

From equation 6.16 we obtain:

$$\frac{\partial T^*}{\partial x}(x) = \frac{\partial P^*}{\partial x}(x)(1+d_P(\frac{\alpha_D}{m_D} - \frac{1-\alpha_D\alpha_P}{l_N})) - \frac{r_N+\alpha_D r_D}{l_N} + \frac{d_P}{\alpha_P}\frac{R(x)}{u_N(x)} \tag{6.18}$$

Thus total system stock T^* always vary with, or in opposition with plant biomass P^*.

6.4. Generalization of the results of model 1 for other trade-offs

We tested the generality of our results from the analysis of our first model by considering other trade-offs that could exist between cycling parameters and soil exploration: a negative relationship between mineralization rate $m_D(x)$ and soil exploration x, and a positive relationship between lixiviation rate $l_N(x)$ in the occupied soil.

We here focus on the calculation of x_P. Most of the other results do not depend on which trade-off is chosen.

The hypothesis of a negative relation between the mineralization rate $m_D(x)$ and soil occupation x is inspired by the fact that mineralization rate within the soil is sensible to root exudation, as in the priming effect case (Kuzyakov et al., 2000). As a consequence, mineralization rate should be higher in a zone of influence with a dense root system than in a sparse root system.

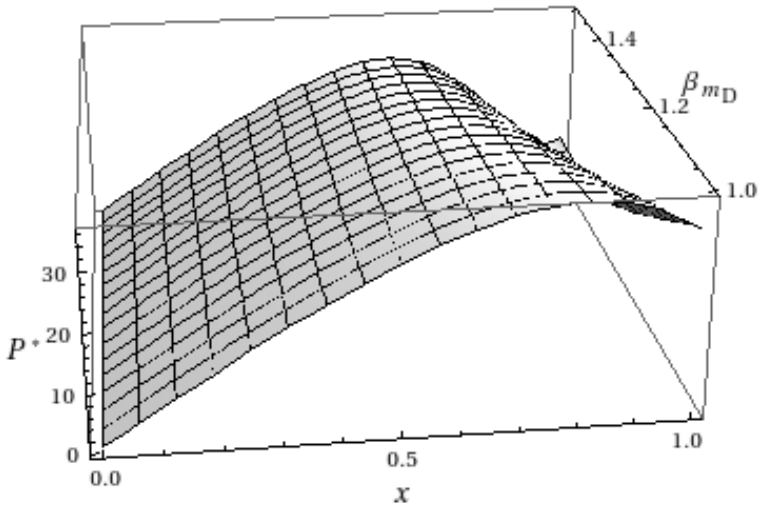
The positive relation between lixiviation rate $l_N(x)$ and x should apply in systems with strong leaching of mineral nutrients. In dense root systems, the mean distance between roots and nutrients is reduced, so that the probability of a nutrient to be lost by lixiviation is lower.

6.4.1. Functional trade-off between soil exploration and mineralization

The trade-off between the mineralization rate and soil exploration is difficult to analyze mathematically, since it affects the partial recycling efficiency α_D. However, numerical

calculations, as illustrated by figure 6.1 show a similar behavior of $P^*(x)$ with x when using this trade-off.

Figure 6.1.: Plant nutrient stock P^* as a function of soil exploration x and trade-off strength β_{MD}. We chose here a convex form for the trade-off, with $m_D(x) = m_D^1(1 + \beta_M D(1-x))$.Lamto parameter are used.



6.4.2. Functional trade-off between soil exploration and lixiviation

If we consider a positive linear relationship:

$$l_N(x) = l_N^1(1 + \beta_{LN}(x-1)) \tag{6.19}$$

We obtain the following expression for x_P:

$$x_P = \frac{R(1) - 1 + \beta_{LN}}{2\,\beta_{LN}} \tag{6.20}$$

Which lead to the following condition for $x_P < 1$:

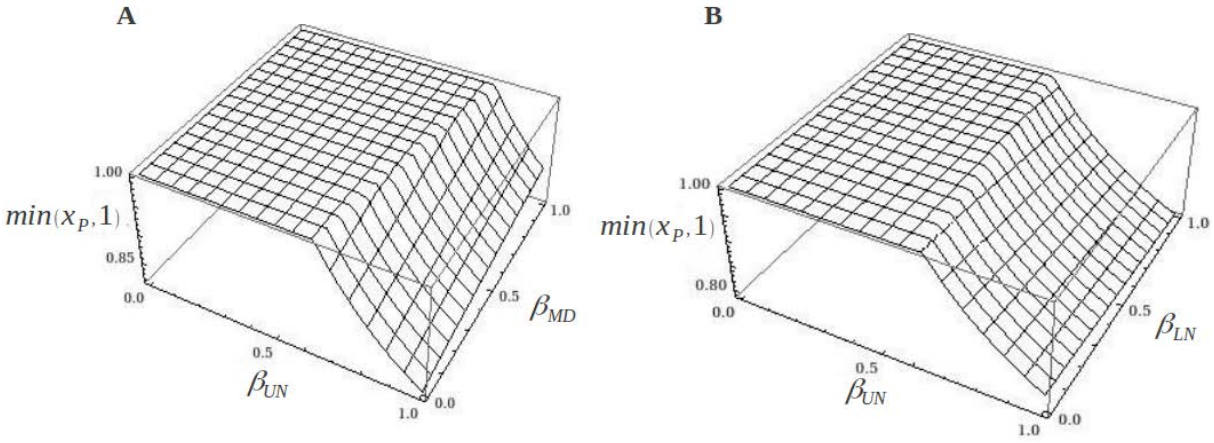
$$R(1) < \beta_{LN} \tag{6.21}$$

As for the trade-offs developed in the main text, restricted exploration is beneficial by low values of $R(1)$ and strong trade-offs (high values of β_{LN}).

6.4.3. Coupled trade-offs

We tested the effect of the existence of several trade-offs by numerical estimations of x_P. The results are presented in figure 6.2. We only tested linear shapes for these trade-offs. In the case tested, there could be either a synergy or an antagonism between the effects of the trade-offs.

Figure 6.2.: $min(x_P, 1)$, the soil occupation value maximizing plant biomass at equilibrium $P^*(x)$ as a function of trade-offs strengths for uptake efficiency (β_{UN}) and mineralization rate (β_{MD}) (panel A) or for uptake efficiency and lixiviation rate (β_{LN}) (panel B).Trade-offs considered here are linear. Lamto parameter are used.



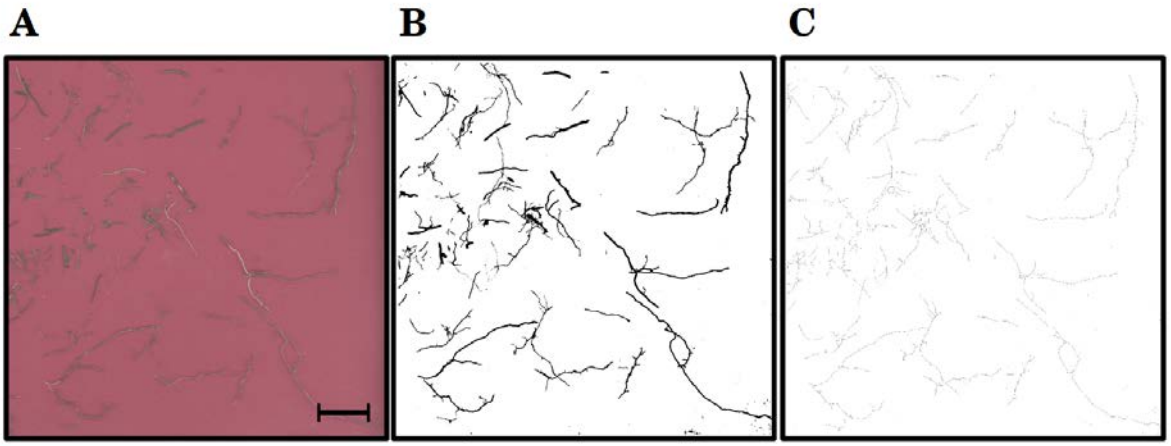
7. Appendix to Chapter 3

7.1. Root scan analysis

Figure 7.1.: imagej script to measure length of roots in a sample spread on a scanner

```
// Imagej script for the measurement of root length
// HP, 12/03/2014

// Open file
filepath=File.openDialog("Selectionnez un fichier.");
open(filepath);
id = getImageID();

// Set scale
run("Set Scale...", "distance="+4722+" known="+20+" pixel=1 unit=cm"); //Set scale in en cm

// Selection of the area to analyze
setTool("rectangle");
waitForUser("Select rectangle");
setBackgroundColor(162, 91, 105);
run("Clear Outside");

// Contrasts roots from the background
run("Enhance Local Contrast (CLAHE)", "blocksize=49 histogram=256 maximum=3 mask=*None* fast_(less_accurate)");
run("HSB Stack");
run("Stack to Images");
selectWindow("Brightness");
close();
selectWindow("Hue");
close();
setAutoThreshold("Default");
run("Threshold...");
waitForUser("Ajust the threshold if necessary and validate.");
run("Make Binary");
run("Convert to Mask");
setForegroundColor(0, 0, 0);
setTool("Paintbrush");
waitForUser("Paint over artefacts");
run("Skeletonize");

// measurement of total root length
run("Measure");

// Visual control of the quality of image
open(filepath);
run("Images to Stack", "name=Stack title=[] use");
```

Figure 7.2.: Steps in the measurement of root length from a scan of dry roots. Panel A shows the original scan of a root sample that was first converted to binary, using an appropriate threshold (panel B). The binary image was then skeletonized (panel C) so that total root length could be calculated from the number of black pixels in the image. The black line on panel A sets the scale of the image (1 cm), 1 pixel = 42 µm.



7.2. Patterns of root exploration

Figure 7.3.: Root mass per unit of soil volume (mr_V) in response to herbivore and fertilisation treatments. The exclosure is figured by the black rectangle, and the fertilised strips are figured by a grey, hatched rectangle (See Figure 3.1A). White box, bare soil; grey box, soils sampled under plants.

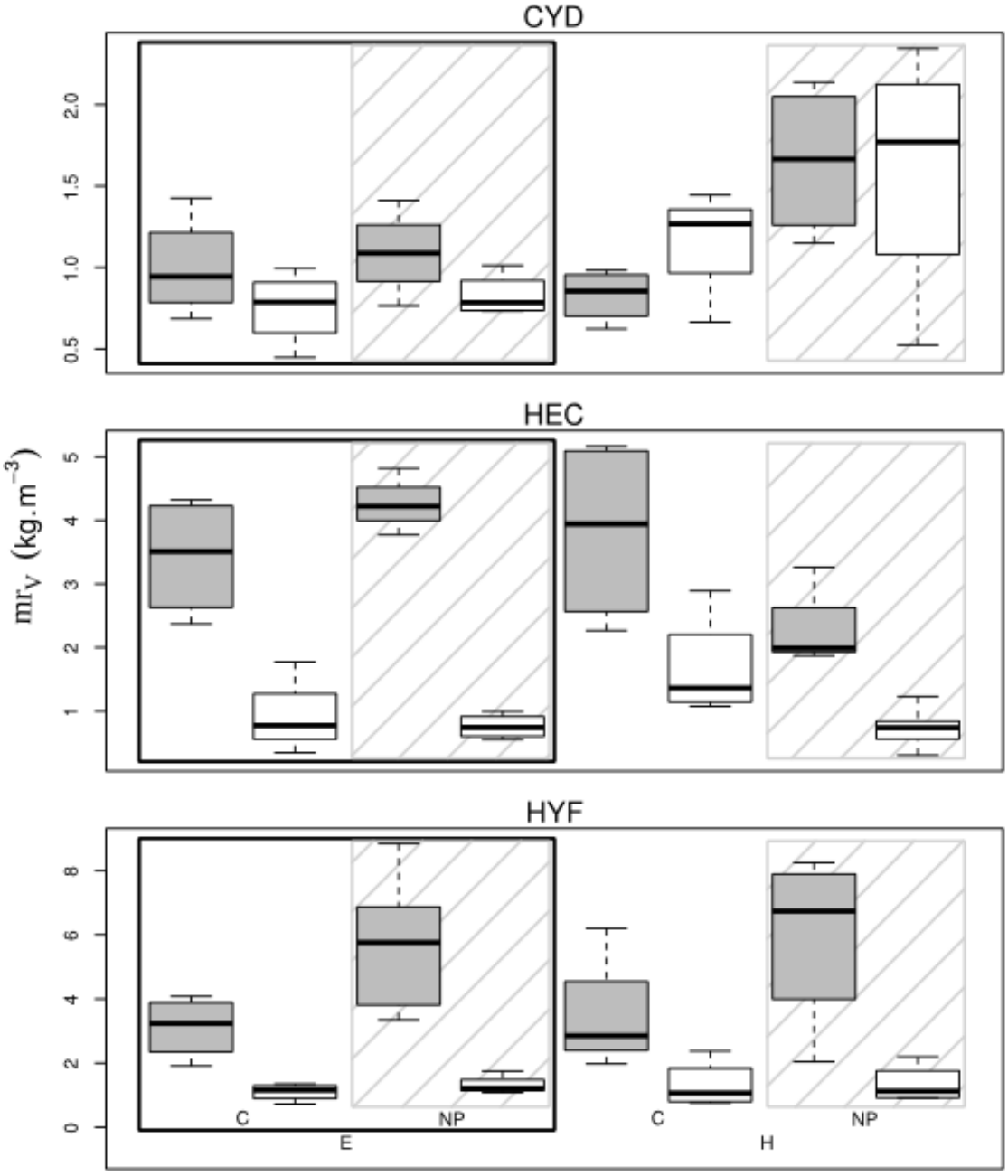


Figure 7.4.: Root mass per unit of soil mass (mr_M) in response to herbivore and fertilisation treatments. The exclosure is figured by the black rectangle, and the fertilised strips are figured by a grey, hatched rectangle (See Figure 3.1A). White box, bare soil; grey box, soils sampled under plants.

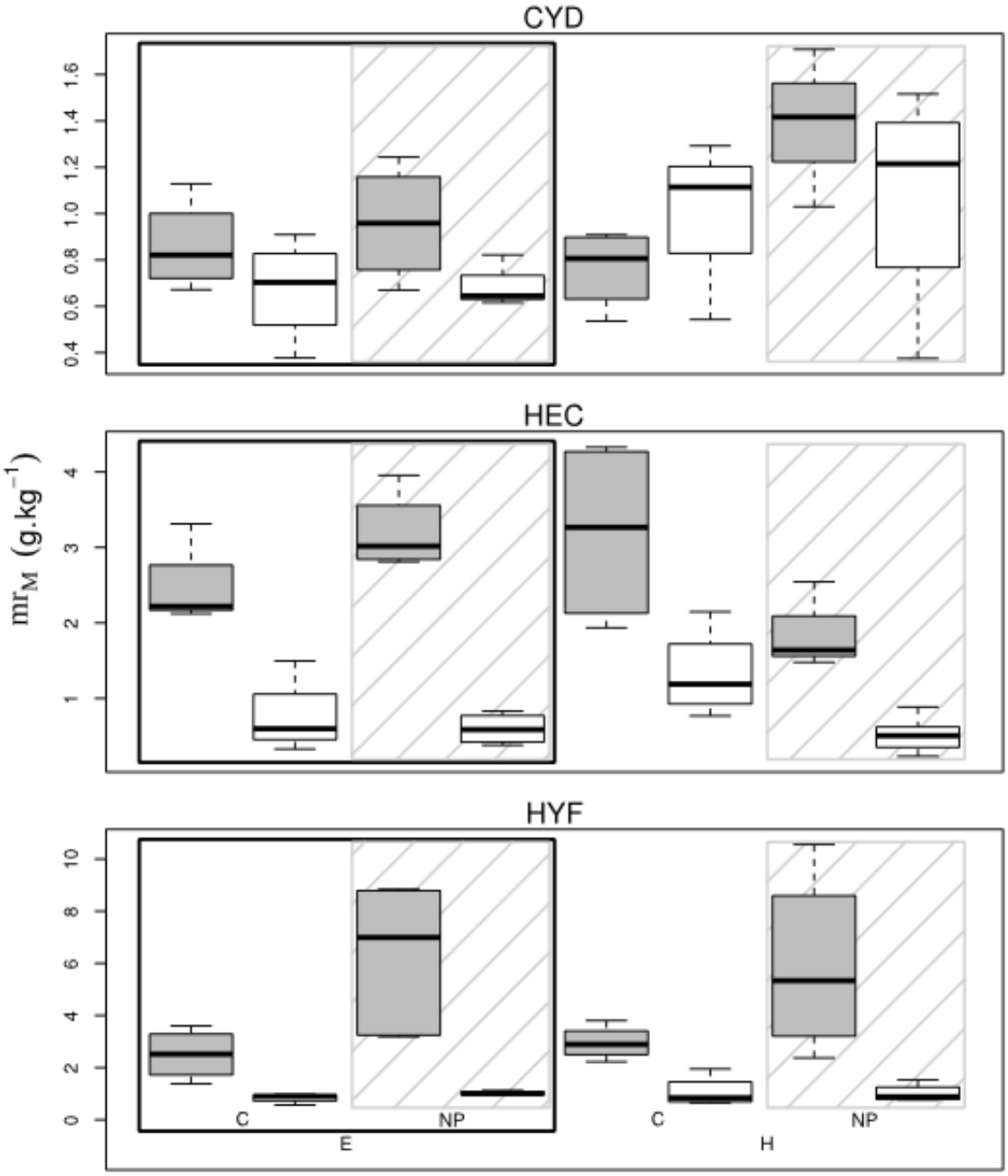


Figure 7.5.: Root length per mass of soil (lr_M) in response to herbivore and fertilization treatments. The exclosure is figured by the black rectangle, and the fertilised strips are figured by a grey, hatched rectangle (See Figure 3.1A). White box, bare soil; grey box, soils sampled under plants.

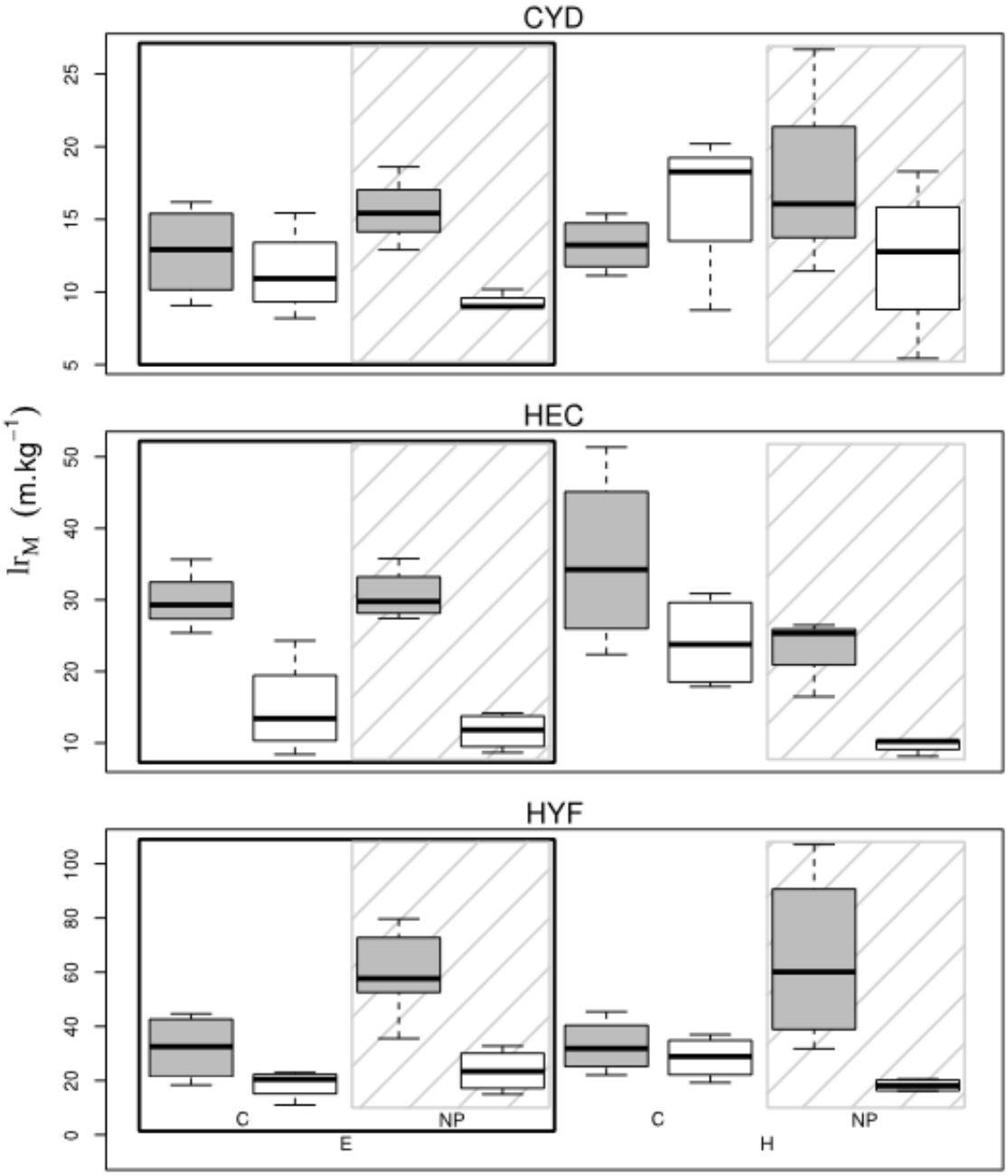


Figure 7.6.: Specific root length (*srl*) in response to herbivore and fertilisation treatments. The exclosure is figured by the black rectangle, and the fertilised strips are figured by a grey, hatched rectangle (See Figure 3.1A). White box, bare soil; grey box, soils sampled under plants.

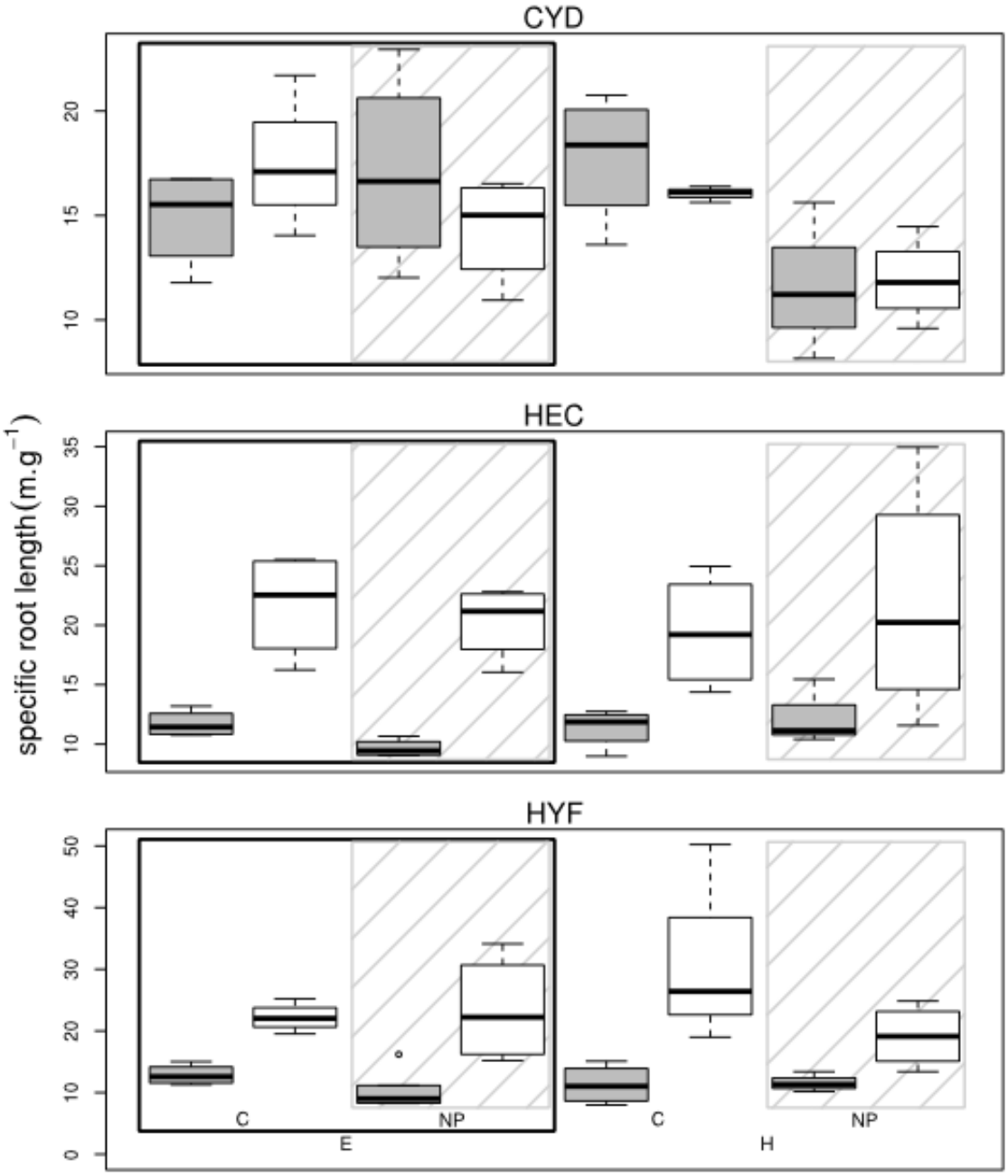


Table 7.1.: Detailed ANOVAs of the minimum adequate models for root densities (drm & drv) and root length densities (lrm & lrv). P-values are summarised by symbols : '***'< 0.001 <'**'< 0.01 <'*'< 0.05 <'.'< 0.1

	mr_M				mr_V		
	numDF	denDF	F-value	p-value	denDF	F-value	p-value
(Intercept)	1	64	21.68	***	67	49.82	***
sp.dom	2	12	20.16	***	12	16.23	***
herbivore	1	1	0.42		1	0.35	
fertilization	1	2	0.83		3	0.85	
cover	1	64	178.17	***	67	155.23	***
sp.dom:fertilization	2	12	5.03	*	12	3.64	.
herbivore:fertilization	1	2	1.66		-	-	-
sp.dom:cover	2	64	28.22		67	28.43	
herbivore:cover	1	64	2.59		67	4.63	*
fertilization:cover	1	64	8.67	**	67	4.79	*

	lr_M				lr_V		
	numDF	denDF	F-value	p-value	denDF	F-value	p-value
(Intercept)	1	65	7482.77	***	66	5552.97	***
sp.dom	2	12	52.97		12	42.05	
herbivore	1	1	0.62		1	0.43	
fertilization	1	2	0.13		2	0.08	
cover	1	65	84.39		66	59.79	
sp.dom:fertilization	2	12	8.13	**	12	4.42	*
herbivore:fertilization	1	2	5.78		2	2.81	
sp.dom:cover	2	65	7.42	**	66	8.42	***
herbivore:cover	1	-	-	-	66	4.52	*
fertilization:cover	1	65	16.94	***	66	9.19	**

7.3. Soil content in C and nutrients

Table 7.2.: Detailed ANOVAs of the minimum adequate models for soil content in C and nutrients.P-values are summarised by symbols : '***'< 0.001 <'**'< 0.01 <'*'< 0.05 <'.'< 0.1

	soil % C				soil % N		
	numDF	denDF	F-value	p-value	denDF	F-value	p-value
(Intercept)	1	69	8.77	**	69	6324.35	***
sp.dom	2	12	0.10		14	0.74	
herbivore	1	1	7.93		1	4.06	
fertilization	1	3	9.96	.	3	14.38	*
cover	1	69	5.08	*	69	6.24	*
sp.dom:fertilization	2	12	2.62		-	-	-
sp.dom:cover	2	69	2.70	.	69	2.04	

	NO_3				NH_4		
	numDF	denDF	F-value	p-value	denDF	F-value	p-value
(Intercept)	1	66	50.745	***	71	501.62	***
sp.dom	2	12	1.448		12	3.04	.
herbivore	1	1	0.010		1	0.89	
fertilization	1	-	-	-	3	14.91	*
cover	1	66	0.337		71	2.79	.
sp.dom:herbivore	2	12	0.874		12	10.06	**
sp.dom:cover	2	66	0.798		-	-	-
herbivore:cover	1	66	0.003		-	-	-
sp.dom:herbivore:cover	2	66	5.031	**	-	-	-

	$[P]_{tot}$				$[P]_{assim}$		
	numDF	denDF	F-value	p-value	denDF	F-value	p-value
(Intercept)	1	70	975.45	***	70	20.59	***
sp.dom	2	10	20.64	***	10	6.40	*
herbivore	1	1	1.17		1	0.10	
fertilization	1	3	34.47	**	3	10.54	*
cover	1	70	7.37	**	70	8.26	**
sp.dom:herbivore	2	10	7.45	*	10	3.39	.
sp.dom:fertilization	2	10	4.18	*	10	5.57	*
fertilization:cover	1	70	5.37	*	70	6.99	*

7.4. plant and soil C:N

7.5. N isotopic data

Table 7.3.: Detailed ANOVAs of the minimum adequate models for CHN and isotopic data on root, soil, leaf and litter. P-values are summarised by symbols : '***'< 0.001 <'**'< 0.01 <'*'< 0.05 <'.'< 0.1

	$\delta^{15}N_{leaf}$				$\delta^{15}N_{litter}$		
	numDF	denDF	F-value	p-value	denDF	F-value	p-value
(Intercept)	1	9	39.67	***	7	6.78	*
sp.dom	2	9	1.21		7	11.21	**
herbivore	1	1	0.17		1	1.00	
fertilization	1	2	10.11	.	2	11.82	.
sp.dom:herbivore	2	9	1.60		7	5.38	*
sp.dom:fertilization	2	9	4.25	.	7	3.46	.
herbivore:fertilization	1	2	1.38		2	0.34	
sp.dom:herbivore:fertilization	2	-	-	-	7	2.88	

	$\delta^{15}N_{root}$				$\delta^{15}N_{soil}$		
	numDF	denDF	F-value	p-value	denDF	F-value	p-value
(Intercept)	1	60	611.407	***	67	3511.37	***
sp.dom	2	8	24.766	***	10	8.08	**
herbivore	1	1	0.834		1	13.65	
fertilization	1	2	4.216		2	0.12	
cover	1	60	11.150	**	67	0.39	
sp.dom:herbivore	2	8	0.215		10	2.25	
sp.dom:fertilization	2	8	4.645	*	10	0.63	
herbivore:fertilization	1	2	0.030		2	1.44	
sp.dom:cover	2	60	0.863		67	0.87	
herbivore:cover	1	60	0.004		67	1.55	
fertilization:cover	1	60	0.291		67	1.82	
sp.dom:herbivore:fertilization	2	8	3.237	.	-	-	
sp.dom:herbivore:cover	2	60	0.377		-	-	
sp.dom:fertilization:cover	2	60	3.082	.	-	-	
herbivore:fertilization:cover	1	60	0.651		-	-	
sp.dom:herbivore:fertilization:cover	2	60	4.031	*	-	-	

Table 7.4.: Detailed ANOVAs of the minimum adequate models for$\Delta\delta^{15}N_{plant-soil}$ for roots and leafs. P-values are summarised by symbols : '***'< 0.001 <'**'< 0.01 <'*'< 0.05 <'.'< 0.1

	$\Delta\delta^{15}N_{root-soil}$				$\Delta\delta^{15}N_{leaf-soil}$		
	numDF	denDF	F-value	p-value	denDF	F-value	p-value
(Intercept)	1	59	657.25	***	62	282.80	***
sp.dom	2	8	9.85	**	7	0.96	
herbivore	1	1	4.21		1	1.07	
fertilization	1	2	7.19		2	15.19	.
cover	1	59	6.44	*	62	0.44	
sp.dom:herbivore	2	8	0.65		7	0.09	
sp.dom:fertilization	2	8	2.44		7	3.15	
herbivore:fertilization	1	2	1.18		2	4.26	
sp.dom:cover	2	59	0.86		62	0.86	
herbivore:cover	1	59	0.18		62	1.69	
fertilization:cover	1	59	1.17		62	1.71	
sp.dom:herbivore:fertilization	2	8	0.73		7	3.28	.
sp.dom:herbivore:cover	2	59	0.17		62	3.44	*
sp.dom:fertilization:cover	2	59	2.99	.			
herbivore:fertilization:cover	1	59	0.40				
sp.dom:herbivore:fertilization:cover	2	59	3.45	*			

8. Appendix to chapter 4

8.1. Relationships between root length density and fluxes of phosphorus whithin the soil

Figure 8.1.: Phosphorus uptake A_P as a function of root density n_{root}, exudation rate e_{cit}, mineral nutrient losses μ_P and soil water content θ.

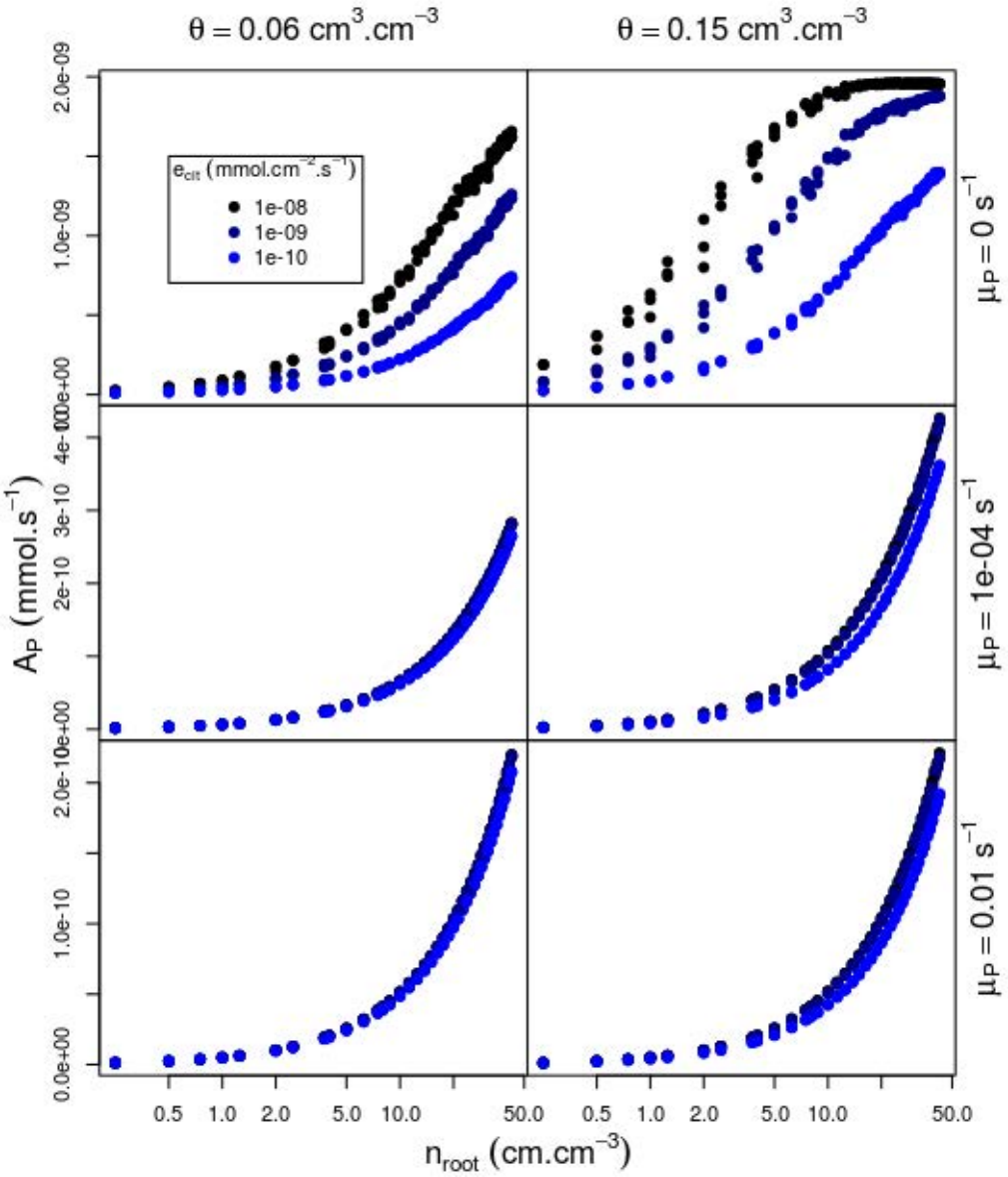
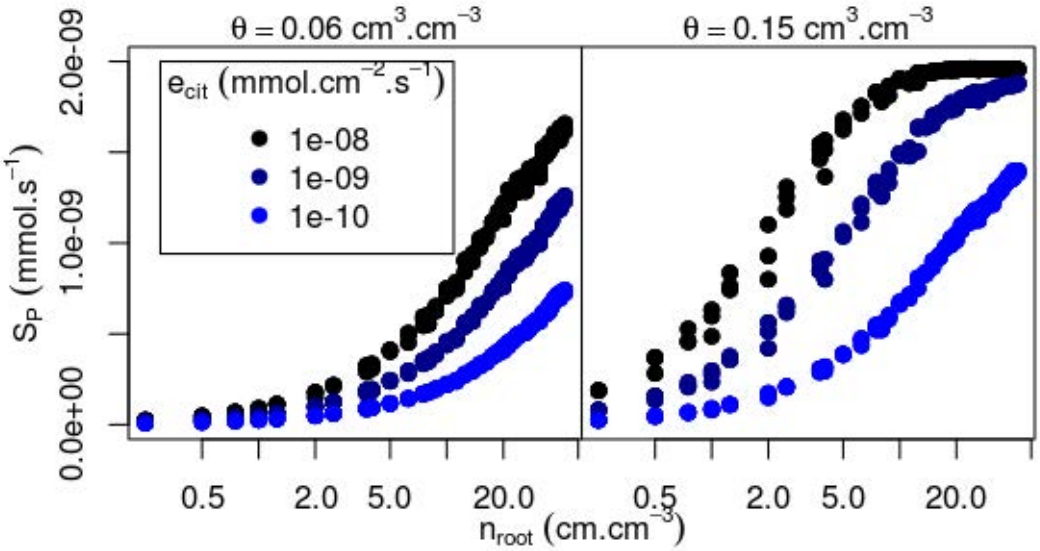
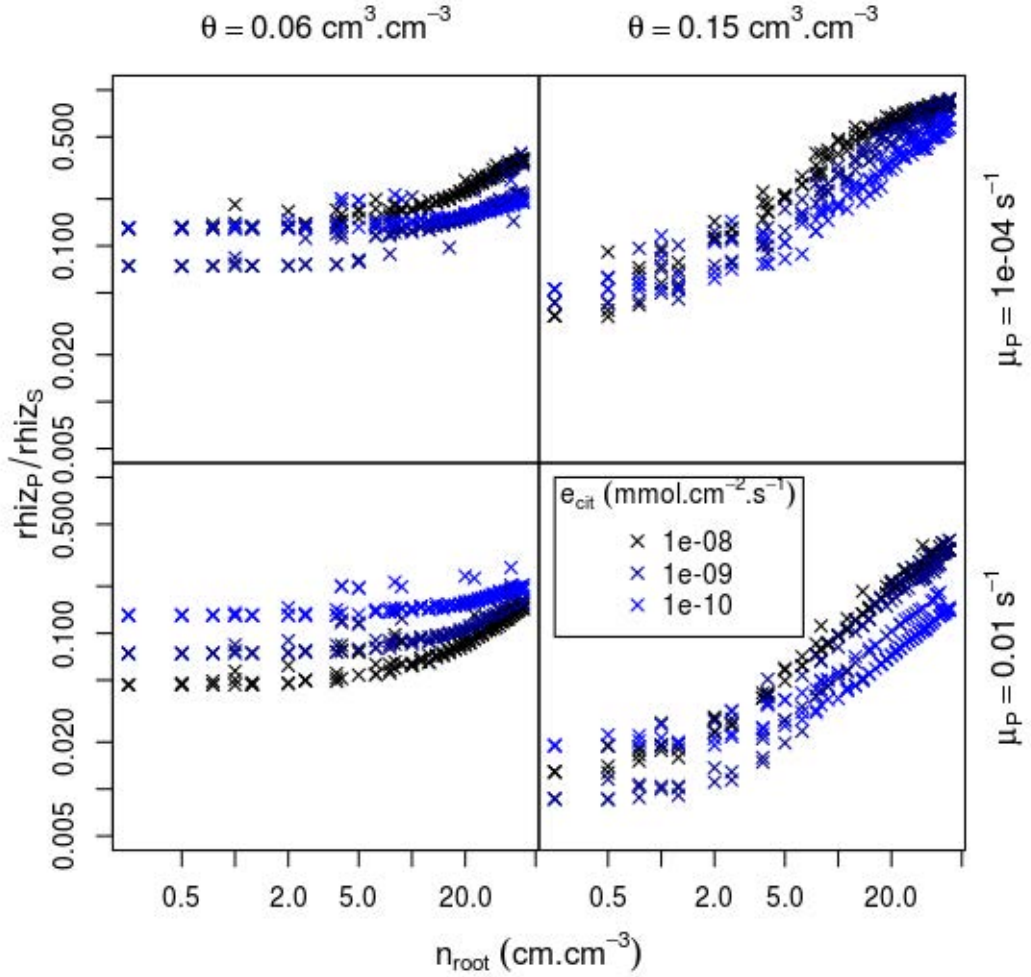


Figure 8.2.: Phosphorus supply S_P as a function of root density n_{root}, exudation rate e_{cit} and soil water content θ.



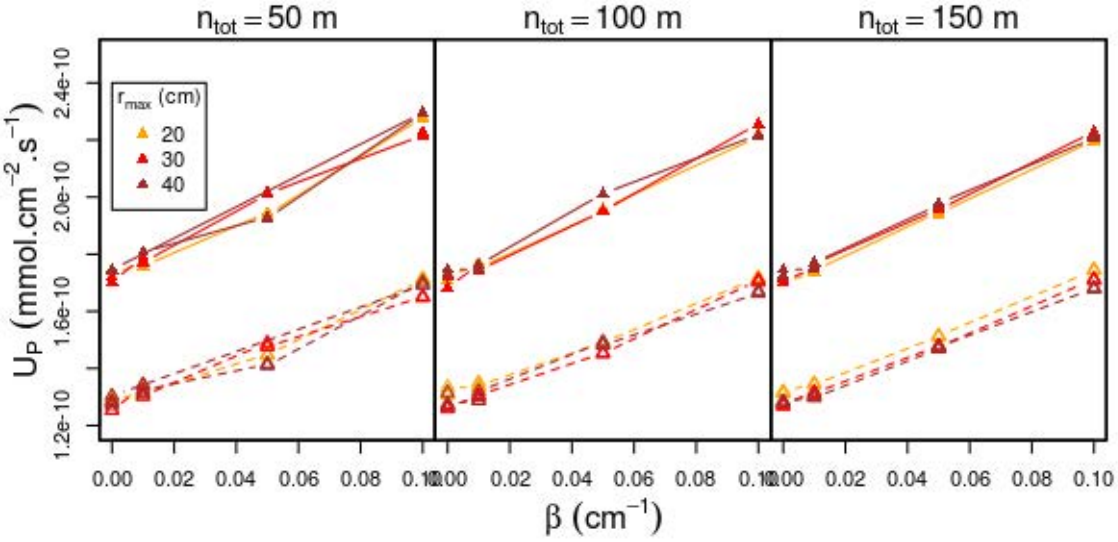
8.2. Relationship between root length density n_{root} and $rhiz_P/rhiz_S$

Figure 8.3.: Ratio of soil occupation ratios $rhiz_P/rhiz_S$ as a function of root density n_{root}, exudation rate e_{cit}, mineral nutrient losses μ_P and soil water content θ.



8.3. Upscaling to the whole plant

Figure 8.4.: Nutrient uptake efficiency U_P as a function of plant exploration parameters: the total length of the root system n_{tot}, the decreasing factor of root density β and maximum root lateral spread r_{max}. We focus here on the case where $\mu_P = 1e^{-4}$ and $\theta = 0.15$, for two exudation rates for which inter-root interactions are either competitive ($e_{cit} = 1e^{-8}$) or facilitative ($e_{cit} = 1e^{-10}$, Cf figure 4.4.1A).



Résumé

La nutrition minérale des plantes dépend à la fois du développement et du fonctionnement de leur appareil racinaire, incluant l'absorption mais aussi la capacité des plantes à influencer les cycles des nutriments, notamment par l'exsudation. Le but de cette thèse est de lier les rétroactions plantes-sol impliquant les cycles des nutriments aux stratégies d'exploration racinaire. Dans la revue bibliographique, je recense des mécanismes d'interaction plantes-sol et leurs échelles spatiales et temporelles. En considérant, à l'échelle de la rhizosphère, les interactions directes entre racines et sol, je propose que la combinaison entre exsudation et absorption des nutriments mène à des synergies entre racines d'une même plante. Ma seconde hypothèse est celle de l'existence d'un compromis entre l'exploration du sol et son occupation (défini comme la capacité des plantes à influencer efficacement le cycle des nutriments). Dans un premier chapitre, je développe un modèle général de recyclage des nutriments afin de déterminer sous quelles conditions les plantes auraient intérêt à limiter leur exploration du sol. Je montre qu'une exploration limitée est une stratégie de nutrition efficace sous certaines conditions, dont l'existence de synergies entre racines et le fait d'être dans un sol pauvre en nutriment. Dans un deuxième chapitre, je mesure le patron d'exploration racinaire et évalue le recyclage de l'azote à l'aide des outils isotopiques, chez trois espèces de Poacées pérennes de la savane de Hwange (Zimbabwe). Cette étude de terrain montre un gradient d'hétérogénéité racinaire entre ces trois espèces. Les Poacées exprimant le patron d'exploration le plus hétérogène ont un cycle de l'azote plus lent, mais potentiellement plus efficace. Dans un dernier chapitre, je développe un modèle mécaniste à l'échelle de la rhizosphère, pour une plante absorbant le phosphore et contrôlant sa disponibilité par l'exsudation de citrate. Je montre que, selon l'échelle d'influence des racines en terme d'exsudation et d'abaissement de la concentration en phosphore, la combinaison de l'exsudation et de l'absorption mène soit à une compétition, soit à une facilitation entre les racines d'une même plante. En me plaçant à l'échelle du système racinaire, je montre que les pertes en phosphore sont limitées par une exploration limitée du sol. Ce dernier résultat va dans le sens du compromis exploration/occupation. Au cours de cette thèse, j'ai donc développé des approches complémentaires, mettant en jeu différents mécanismes et échelles d'interactions plantes-sol. Le fait que les racines ne se limitent pas à un rôle d'absorption, mais agissent activement sur les cycles de nutriments a mené à deux résultats originaux : la facilitation inter-racinaire et intra-plante, et le fait qu'une exploration limitée puisse être considérée comme une stratégie efficace de nutrition. Enfin, ce travail souligne l'importance d'intégrer les divers mécanismes d'interaction plantes-sol pour comprendre les stratégies de nutrition des plantes et mieux prédire leur impact sur les cycles de nutriments à l'échelle des écosystèmes.

Mots clés : *stratégies d'exploration racinaire ; zone d'influence souterraine ; rhizosphère ; cycles des nutriments ; rétroactions plantes-sol ; abondance naturelle du ^{15}N ; modélisation ; compromis ; facilitation racinaire intra-plante*

Abstract

Plant nutrition depends on complementary mechanisms: the development of root systems, root uptake and plant ability to control nutrient cycling, e.g. through exudation. The aim of this thesis is to link plant-soil feedbacks involving the cycling of nutrients and root foraging strategies. I first review the different mechanisms of plant influence on nutrient cycling within the soil and assess their respective scales. Considering the direct effect of roots on the soil at the scale of the rhizosphere, I hypothesize that the combination of absorption and exudation may lead to synergies between the roots of a plant. At the scale of the whole root system, I propose a second, heuristic hypothesis: the existence of a trade-off between soil exploration and soil occupation (defined as the ability of plants to influence efficiently nutrient cycling). In a first chapter, I develop a general model of nutrient cycling, to determine under which condition plants should limit the exploration of soil by their roots. I show that limited exploration is an efficient strategy under specific conditions, especially nutrient-poor soils and the existence of synergies between roots. In a second chapter, I characterize soil occupation and nitrogen cycling, by the use of isotopes ratios, in the plant-soil system of three perennial grasses of the savanna of Hwange (Zimbabwe). This field study shows a gradient of root heterogeneity among these grass species. Those showing the more heterogeneous root pattern have a slower but potentially more efficient nitrogen cycling. In a last chapter, I develop a numerical mechanistic model at the rhizosphere scale for a plant taking up phosphorus and increasing its availability through exudation of citrate. I show that, depending on the extent of root influence on soil by exudation and nutrient depletion, competition between roots as well as facilitation arise from the combination of root uptake and exudation. By upscaling rhizosphere processes to the root system, I show that phosphorus losses are minimized by a restricted soil exploration, which backs the hypothesis of a trade-off between soil exploration and occupation. Overall, I developed complementary approaches that took into account several mechanisms and scales of plant-soil interactions. Considering that root functions are not limited to nutrient uptake, but also involve their influence on nutrient cycling, lead to two novel results: the potential existence of intra-plant and inter-root facilitation, and limited soil exploration as an efficient foraging strategy. This work underlines the importance of accurately integrating the mechanisms of plant-soil interaction to assess their nutrient strategies and to predict their impact on nutrient cycling within ecosystems.

keywords: *root foraging strategies; belowground zone of influence; rhizosphere; nutrient cycling; plant-soil feedbacks; ^{15}N natural abundance; modeling; trade-off; intra-plant root facilitation*